A survey of the last instar larvae of the Lycaenidae (Lepidoptera) of California

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Abstract. The biology and last instar larval morphology of 69 species of California lycaenids are surveyed. Diagnostic descriptions of the subfamilies, genera, and species are provided together with a species key based primarily on larval morphology. Also included is a list of confirmed larval hosts including many host species not previously reported. Major aspects of the larval morphology of 29 exotic lycaenid species representing six subfamilies and 17 tribes are also reviewed for comparison.
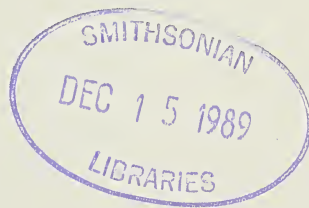
Introduction

This is the first in a series of surveys of the mature larvae of the butterfly fauna of California. Included are 69 species of Lycaenidae which are listed in Appendix 1. Future works will survey the larvae of the Hesperiidae, Nymphalidae, Papilionidae, and Pieridae of California.

The Lycaenidae is perhaps the largest family of butterflies with nearly 40% of known butterfly species (Vane-Wright, 1978). The most recent comprehensive review of the group (based largely on adult characters) divides it into eight subfamilies excluding the Riodinidae (Eliot, 1973). Miller and Brown (1981) and Stehr (1987) also accord separate family status to the Riodinidae in spite of its placement as a subfamily of Lycaenidae by other authors (Ehrlich, 1958; Vane-Wright, 1978; Ackery, 1984; Scott, 1986). The classification of Eliot (1973) is retained here except that the Riodininae is considered subordinate to the Lycaenidae. Thus, the California lycaenids are divided into four subfamilies: Lycaeninae, Polyommatinae, Riodininae, and Theclinae. This arrangement is provisional and based largely on convenience, since most workers are familiar with these groups. Certainly these 'subfamilies' are not phylogenetically equivalent; a more precise hierarchic classification based on adult, larval, and biological characteristics awaits a broader faunistic survey beyond the scope of this work.

Although the life histories of nearly all species treated in this key have been published, most are inadequate for larval identification. The majority of larval descriptions have relied heavily on coloration with little attention to structural features. But color is perhaps the least reliable tool for identification since larvae of many species have similar coloration, some (especially polyphagous) species have multiple color morphs, and ground color may change in response to different food substrates (Orsak and Whitman, 1987). Also, larvae preserved in fluids often lose pigmentation; only melanic pigments associated with sclerotized structures such as the head, legs, and setae are resistant to fading.

Overall the most reliable characters for identifying larvae are structural. The presence, absence or condition of various organs and specialized setae are often diagnostic for higher taxa; the size, structure, and distribution of specific types of setae and other cuticular structures are often diagnostic for genera and species. Some species cannot be identified reliably by morphological traits but larval host, habitat, and locality data may provide additional clues to their identity.

Due to the paucity of detailed descriptions of larvae of the taxa treated in this work, a diagnostic description of each genus and a table of comparative characters for all species are included (Table 1). Some of the characters employed in these descriptions are new or poorly described in the literature and much of the terminology has not been standardized; therefore, a discussion of larval morphology and character terminology (with a glossary) is included. This discussion is not exhaustive but deals mostly with those characters found to be useful for identifying the species treated here.

Table 1.   Comparative characters of california lycaenid larvae

Species	I.[1]	H.G.	E.T.	L.C.	M.S.	D.S.	H.W.	B.L.	N
Riodininae									
A. mormo	5	-	-	-	5	-	2.28	15	10
" *palmerii*	5	-	-	-	5	-	1.78	12	2
C. nemesis	5	-	-	+	4	-	1.45	16	9
" *wrighti*	5	-	-	+	4	-	1.60	14	6
Lycaeninae									
L. arota	4	-	-	+	2	-	1.61	17	10
" *cupreus*	4	-	-	+	2	-	1.26	17	8
" *editha*	4	-	-	+	3	+	1.67	18	10
" *gorgon*	4	-	-	+	2-3	-	1.74	18	10
" *helloides*	4	-	-	+	2	-	1.44	15	10
" *hermes*	4	-	-	+	2	-	1.31	15	5
" *heteronea*	4	-	-	+	2-3	+	1.63	18	10
" *mariposa*	4	-	-	+	2	-	1.53	15	3
" *nivalis*	4	-	-	+	2	-	1.42	20	10
" *phlaeas*	4-5	-	-	+	2	-	1.46	19	10
" *rubidus*	4	-	-	+	3	+	1.69	18	10
" *xanthoides*	4	-	-	+	3-5	+	1.87	24	10
Theclinae									
A. halesus	4	+	-	-	2	-	2.34	22	10
C. (C.) comstocki	4	+	-	-	2	+	1.17	15	9
" " *dumetorum*	4	+	-	-	2	+	1.42	19	10
" " *lemberti*	4	+	-	-	2	+	1.39	17	2
" " *perplexa*	4	+	-	-	2	+	1.33	15	10
" *(I.) augustus*	4	+	-	-	2	+	1.24	14	10
" " *eryphon*	4	+	-	-	2	+	1.75	17	9
" " *fotis*	4	+	-	-	2	+	1.16	16	10
" " *mossii*	4	+	-	-	2	+	1.40	18	10
". *(M.) johnsoni*	5	+	-	-	2	+	1.59	17	3
" " *loki*	5-7	+	-	-	2	-	1.62	16	10
" " *nelsoni*	5-7	+	-	-	2	-	1.55	15	10
" " *siva*	5-7	+	-	-	2	-	1.72	16	10
" " *spinetorum*	5	+	-	-	2	+	1.85	21	10
" " *thornei*	5-7	+	-	-	2	-	1.51	15	3
H. grunus	4	-	-	+	5	-	1.78	17	10
H. titus	4	+	-	-	6	+	2.02	24	4
M. leda	4	+	-	-	2	+	1.03	12	10
S. auretorum	4	+	-	-	3	+	1.56	18	10
" *behrii*	4	+	-	-	2	+	1.19	14	10
" *californica*	4	+	-	-	2	+	1.50	17	2
" *fuliginosum*	4	+	-	-	3	+	1.58	21	10
" *saepium*	4	+	-	-	2	+	1.44	17	10
" *sylvinus*	4	+	-	-	3	+	1.57	17	10
" *tetra*	4	+	-	-	3	+	1.78	19	10
S. avalona	4	+	-	-	2	+	1.15	13	6
" *columella*	4	+	-	-	2	+	1.11	14	10
" *melinus*	4	+	-	-	2	+	1.22	16	10
Polyommatinae									
A. franklinii	4	-	-	-	2	-	.86	13	3
B. exilis	4	+	+	-	2	-	.66	11	10
C. argiolus	4	+	+	-	2	+	.89	12	10

Table 1. con't

Species	I.[1]	H.G.	E.T.	L.C.	M.S.	D.S.	H.W.	B.L.	N
E. battoides	4	+	+	-	2	+	.63	9	10
" *enoptes*	4	+	+	-	2	+	.67	10	10
" *mojave*	4	+	+	-	2	+	.68	9	10
" *rita*	4	+	+	-	2	+	.60	10	10
E. amyntula	4	+	+	-	2	+	1.03	14	10
" *comyntas*	4	+	+	-	2	+	.83	12	4
G. lygdamus	4	+	+	-	2	+	1.11	19	10
" *piasus*	4	+	+	-	2	+	1.17	18	10
H. ceraunus	4	+	+	-	2	+	.73	12	10
" *isola*	4	+	+	-	2	-	.71	11	10
I. acmon	4	+	+	-	2	+	.77	11	10
" *icarioides*	4	+	+	-	2	+	1.03	17	10
" *lupini*	4	+	+	-	2	+	1.00	15	10
" *neurona*	4	+	+	-	2	+	.89	12	10
" *shasta*	4	+	+	-	2	+	.85	12	10
L. marina	4	+	+	-	2	+	.75	11	10
L. idas	4	+	+	-	2	+	.90	14	2
" *melissa*	4	+	+	-	2	+	1.00	16	10
P. sonorensis	4	+	+	-	2	+	1.10	17	10
P. speciosa	4	+	-	-	2	+	.65	10	10
P. saepiolus	4	+	+	-	2	+	.95	12	6
P. emigdionis	5-7	+	+	-	2	+	1.27	16	10

[1] I = larval instars; H.G. = honey gland; E.T. = eversible tubercles; L.C. = lateroseries of crochets; M.S. = mandibular setae; D.S. = dendritic setae; H.W. = mean head width (mm); B.L. = mean body length (mm); N = number of specimens measured for H.W. and B.L.; + = present, - = absent.

In order to understand better the distribution of morphological characters among higher taxa, larvae of several exotic species were also examined. Table 2 compares the following exotic species with respect to eight major morphological characters: Liphyrinae: *Liphyra brassolis* Westwood from Australia; Lycaeninae: *Heliophorus epicles* (Godart) from Malaysia; Miletinae: *Feniseca tarquinius* (Fabricius) from Illinois, *Spalgis epeus* (Westwood) from Thailand; Polyommatinae: *Anthene seltuttus affinis* (Waterhouse and Turner) and *Candalides xanthospilos* (Hübner) from Australia, *Everes argiades* (Palla) from Japan, *Erysichton lineata* (Murray), *Danis hymetus* (C. and R. Felder), *Lampides boeticus* (Linnaeus), *Syntarucus plinius* (Fabricius), a *Xylomelum*-feeding member of the *Theclinesthes miskini* (T.P. Lucas) — *onycha* (Hewitson) complex, and *Zizina labradus* (Godart) from Australia, and *Zizula hylax* (Fabricius) from Thailand; Riodininae: *Melanis pixe* (Boisduval) from Texas and *Zemeros flegyas* (Cramer) from Thailand; Theclinae: *Arhopala centaurus* (Fabricius) and *Cheritra freja* (Fabricius) from Thailand, *Deudorix epijarbas* (Moore) from Australia, *Erora quaderna* (Hewitson) from Arizona, *Eumaeus atala* (Poey) from Florida, *Flos areste* (Hewitson)

Table 2. Comparative larval features for some exotic lycaenidae

Species[1]	H.G.	E.T.	L.	S.L.	L.C.	M.S.	S.S.	Chalazae
Riodininae								
Hamearini								
Z. flegyas	-	-	+	+	+	2	+	simple
Riodinini								
M. pixe	-	-	+	+	+	24	+	simple
Liphyrinae								
L. brassolis	-	-	-	+	+	2	-	stellate
Lycaeninae								
H. epicles	-	-	+	+	+	4	+	simple
Miletinae								
F. tarquinius	-	-	+	+	-	2	-	simple
S. epeus	-	-	+	+	+	1	-	simple
Theclinae								
Arhopalini								
A. centaurus	+	+	+	+	+	5	+	buttressed
F. areste	+	+	+	+	+	6	+	buttressed
S. quercetorum	+	+	+	+	+	4	+	buttressed
Cheritrini								
C. freja	-	-	+	+	+	2	?	buttressed
Deudorigini								
D. epijarbas	+	-	+	+	-	3	+	buttressed
Eumaeini								
E. quaderna	-	-	+	+	-	2	+	stellate
E. atala	-	-	+	+	-	2	+	buttressed
Hypolycaenini								
H. erylus	+	-	+	+	+	2	+	buttressed
Luciini								
Hypochrysops sp.	+	+	+	+	+	4	+	simple
P. kamerungae	-	-	+	+	+	6	+	buttressed
Ogyrini								
O. genoveva	+	+	+	+	+	5	+	buttressed
Theclini								
H. crysalus	-	-	+	+	+	6	+	buttressed
Zesiini								
P. chlorinda	+	+	+	+	+	5	+	buttressed
Polyommatinae								
Candalidini								
C. xanthospilos	+	+	+	+	-	2	+	buttressed
Lycaenesthini								
A. seltuttus	+	+	+	+	-	2	+	simple
Polyommatini								
E. argiades	+	+	+	+	-	2	+	stellate
E. lineata	+	+	+	+	-	2	+	stellate
D. hymetus	+	-	+	+	-	2	+	stellate
L. boeticus	+	+	+	+	-	2	+	stellate
S. plinius	+	+	+	+	-	2	+	stellate
T. miskini-onycha	+	+	+	+	-	2	+	stellate
Z. labradus	+	+	+	+	-	2	+	stellate
Z. hylax	+	+	+	+	-	2	+	simple

[1] Complete citations in text; H.G. = honey gland; E.T. = eversible tubercles; L. = lenticles; S.L. = spatulate lobe on prolegs; L.C. = lateroseries of crochets; M.S. = mandibular setae; S.S. = sensory setae; + = present, - = absent, ? = presence or absence not determined.

from Malaysia, *Hypaurotis crysalus* (Edwards) from Arizona, *Hypo-chrysops apelles* (Fabricius) from Australia, *Hypolycaena erylus* (Godart) from Thailand, *Ogyris genoveva* Hewitson, *Philiris kamerungae* Water-house, and *Pseudalmenus chlorinda* (Blanchard) from Australia, and *Surendra quercetorum* (Moore) from Thailand.

The keys, diagnostic tables, and descriptions are based on observations by the authors of live and/or preserved larvae and photographs. Descriptions of genera and higher taxa are based on the California fauna except where noted. Distributional data has been compiled from several sources including publications and private collectors. Larval color descriptions are based on living material and/or color photographs.

Host plant information presented in the diagnostic section is based on published records and field observations by the authors; only relatively recent literature citations are given. Appendix 2 lists only those hosts confirmed by the authors' field collections; some reconfirm old records but many are new. The authors of botanical names are abbreviated according to the format of Munz and Keck (1959).

The majority of larvae examined were collected in the field by the authors or reared from ova from field collected adults. Larval morphology was determined primarily using a binocular dissecting microscope. The fine structures of some organs were further examined using a compound microscope with fiber-optic illumination and/or a scanning electron microscope (SEM). The orientation of line drawings and SEM photographs used for illustration are standardized (unless otherwise indicated) with cephalad to the left (lateral views) or top (dorsal views).

The key and descriptions apply to last instar larvae. Although the number of larval instars in some Lepidoptera may depend upon environmental variables and diet, most California lycaenids appear to have a constant number of instars. Most species have four instars but the riodinines, one polyommatine, and six theclines typically have five or more instars. In the Lycaenidae the last instar often differs morphologically from previous instars. Since the instar in which various organs and specialized setae first appear varies for different taxa, the best general means of determining the instar is larval size. Although body length increases within an instar, sclerotized body regions such as the head remain constant in size between molts.

The head width for last instar larvae of each species is included in Table 1 along with the body length (from anterior margin of the prothorax, excluding the neck, to the caudal margin of abdominal segment 10) to aid in determining larval instar and to indicate comparative size among species. All measurements are in millimeters and are based on preserved larvae. For most species these values are derived from a single collection or pooled collections of ten individuals representing a single population. Different preservation methods, as well as larval condition at the time of preservation, can result in different body length and width dimensions. The problem of morphological variability

among subspecies is discussed for a few species where it may aid in identification. A broader discussion of all subspecies is beyond the scope of this work.

The most effective use of the key requires a binocular dissecting microscope since major emphasis is placed on small morphological features. Whenever possible one should attempt to identify larvae while they are alive because some structures are best seen while the larval surface is dry and because coloration may be useful.

There are several effective techniques for larval preservation; the most important considerations are to distend the larva and fix the tissues. Commonly larvae are killed in KAAD (kerosene, ethanol, acetic acid, and dioxane) or other fluids which both distend and fix them. Another satisfactory method is to inject the larva through the anal opening with a fixative such as Kahle's fluid until it is sufficiently distended and/or fix it in hot water (70-85 degrees C.) for about five minutes. Larvae are usually stored in 70-80% ethanol; they should not be put into alcohol until they have been properly fixed. Inflated, freeze-dried, and critical point-dried larvae are also satisfactory for identification but may be difficult to store and handle. Dry or shriveled larvae, larval exuviae, and carcasses remaining after parasite emergence may be identifiable after softening in 5% potassium hydroxide solution. For a broader discussion of methods for larval preservation see Peterson (1948) or Stehr (1987).

LARVAL MORPHOLOGY

The immature stages of many species of Lycaenidae are commonly associated with ants. This association is reflected in the specialized morphology of the larvae among which a variety of myrmecophilous adaptations have evolved (see Hinton, 1951; Henning, 1983b; Cottrell, 1984; Kitching and Luke, 1985).

The known mature larvae of most lycaenids (including nearly all California species) share a few morphological features which (in combination) distinguish them from all other Lepidoptera. The presence of cuticular lenticles and a fleshy terminal lobe on the prolegs are almost unique to this family where they occur in most known species. Other distinctive features such as an onisciform body shape, retractable head, eversible tubercles, and honey gland are somewhat less widely distributed in the Lycaenidae. The full extent of the distribution of these and other diagnostic features remains speculative since the larvae of most species remain undescribed. Generalizations are further hindered by the morphological diversity encompassed by those species which have been investigated.

A clearer understanding of the relationships among higher taxa in the Lycaenidae can probably by gained by broad faunal surveys of their immature stages as suggested by Henning (1983a), Cottrell (1984), and De Vries et al (1986), yet few such works exist. Malicky (1969a, 1969b, 1970) surveyed the larval morphology (especially ant-associated organs) of Central European lycaenids and produced a key based on their morphology, coloration, and host plants. Scott (1986) produced a last instar larval key to the families, subfamilies, and some tribes of North American butterflies; his key is more detailed than those of Peterson (1948) and Stehr (1987), which pertain to all North American Lepidoptera, but fails to consider the full range of diversity in North American lycaenids.

The shape of lycaenid larvae is often termed onisciform (shaped like a sowbug or woodlouse, *Oniscus*). The prothorax (T1) is often the longest segment since in most species the head is retractable into it. The body is usually broadest and highest at the mesothorax (T2), metathorax (T3), or first abdominal segment (A1) and gradually tapered posteriorly. Abdominal segments ten (A10), nine (A9), and (usually to a much lesser extent) eight (A8) are fused to varying degrees in different groups. In cross-section the body is typically convex dorsally and flattened ventrally. The dorsum may be evenly rounded but in some species paired dorsal prominences (flanking the middorsal line) create a trapezoidal outline in cross-section and a saw-toothed lateral profile. Middorsal prominences occur in some exotic species such as *Cheritra freja* of southeast Asia. The junction of the lateral and ventral body regions typically forms a fleshy lateral fold (often fringed with long setae) which conceals the legs when at rest. When inflated (as commonly occurs during preservation) the body may assume a more cylindric shape

typical of other Lepidoptera. An onisciform body is typical of the subfamilies Curetinae, Liphyrinae, Lycaeninae, Polyommatinae and Theclinae; but the larvae of some Miletinae and many Riodininae are much less onisciform while those of the exotic Lipteninae and Poritiinae are not at all (Cottrell, 1984).

The lycaenid larval head is commonly much narrower than the thoracic segments and attached to a neck-like extension of the prothorax into which it can be withdrawn. The size of the head relative to body width, the neck length, and degree to which the head can be withdrawn are variable among (and to a lesser degree within) the lycaenid subfamilies. Among the California fauna the head is smallest and neck generally longest in the Polyommatinae while the head is largest and neck shortest in the Riodininae. A broad nonretractable head is typical of the known larvae of Riodininae and of some other subfamilies such as the Miletinae (including *Feniseca tarquinius* of eastern North America) and of the Florida thecline *Eumaeus atala*.

Other morophological features common to mature lycaenid larvae include the presence of prolegs on A3-A6 and A10 (anal prolegs) and numerous secondary setae. Also, with few exceptions the crochets on the prolegs are arranged in a mesoseries divided by a fleshy lobe (fig. 72); some species also have a lateroseries of crochets (fig. 72a). Most known lycaenids, including all California species, possess a well defined prothoracic shield (fig. 1). A well developed (sclerotized) suranal shield is present in many exotic species but not in California lycaenids; a poorly developed suranal shield is present in the riodinines and in *H. grunus*.

Many lycaenids in the Curetinae, Liphyrinae, Polyommatinae, and Theclinae possess a pair of eversible tubercles on the eighth abdominal segment (fig. 1, 20) and/or a honey gland (Newcomer's organ) usually located on the seventh abdominal segment (figs. 1, 19). In the Southeast Asian thecline, *H. erylus*, the honey gland is located on the eighth abdominal segment. Analogous structures are present in some exotic riodinines such as *Anatole rossi* Clench which has paired eversible tubercles on the metathorax and paired eversible honey glands on the eighth abdominal segment (Ross, 1964). Honey glands produce a fluid which ants imbibe while the eversible tubercles may either attract or excite ants by releasing semiochemicals which mimic the ants' own pheromone(s) (Henning, 1983a and b). Cuticular lenticles, which probably occur in most lycaenids (see lenticle discussion below), apparently also have a chemical communication function (Malicky, 1970; Henning, 1983a and b).

A few characters permit an easy distinction between the larvae of riodinines and other lycaenids in California. Among the riodinine larvae the longest setae are clustered in tufts or verrucae (figs. 30, 31, 69, 70) and are frequently longer than the head width; the prothoracic shield is transverse (the length along the dorsal midline is about half as

great as the width) and adorned with several conspicuously long setae which extend anteriorly over the head (fig. 5). Perhaps the best distinguishing feature of the riodinine larvae is the anteroventral displacement of the A1 spiracles to a location just anterior and slightly ventral to the lateral verrucae (figs. 30, 69, 70) where they may be concealed by a cuticular fold; spiracles on the other abdominal segments are located about midway between the dorsal and lateral verrucae. This condition probably applies to most New World riodinines (Don Harvey, 1987 and *in litt.*), but not to the Old World taxa. Among the larvae of other California lycaenids all setae are shorter than the head width and randomly scattered over the body; the prothoracic shield is often approximately diamond-shaped (figs. 33-54, 61, 64, 67, 71) and is usually as long or longer than wide; no setae on the shield extend forward as far as the anterior margin of the prothorax (fig. 1).

Some exotic riodinines possess additional features which apparently do not occur in other Lepidoptera families. For example, the neotropical species *A. rossi* (Clench), *Audre epulus signatus* (Stichel), and *A. susanae* (Orfila) have a pair of vibratory papillae on the prothorax and paired honey glands on the eighth abdominal segment (Ross, 1964; Bruch, 1926; and Bourquin, 1953, respectively). Larvae of *A. rossi* also possess a pair of eversible tubercles on the metathorax (Ross, 1964). The aforementioned species are notably myrmecophilic, unlike the California riodinines.

Chaetotaxy is the primary tool for identifying most Lepidoptera larvae yet detailed systematic descriptions of lycaenid larval chaetotaxy are uncommon. Clark and Dickson (1956b) proposed the use of first instar setal patterns as a tool for elucidating phyletic relationships in the Lycaenidae and later (1971) described the early stages of the South African fauna. Other workers (Lawrence and Downey, 1966; Downey and Allyn, 1979 and 1984; and Wright, 1983) provided detailed descriptions of four North American species. In each of the latter works a modified version of Hinton's (1946) setal nomenclature was employed to describe (primarily) the first instar chaetotaxy. These authors also recognized a variety of structural forms of setae, some of which were found only in later instars.

Hinton (1946) recognized two functional types of setae in the order Lepidoptera: **microscopic** or proprioreceptor setae located along intersegmental folds and where different body parts make contact, and long or **tactile** setae which are more widely distributed and may be modified for specialized functions. The microscopic setae have received little attention by investigators due to their small size while the structure and distribution of tactile setae are widely employed in identifying larvae of many families of Lepidoptera.

Tactile setae may be further categorized as **primary, subprimary,** and **secondary.** Primary setae, found in specific body locations, are believed to represent the archetypal lepidopteran setal pattern and, with few

exceptions, are discernible at least in the first instar. Subprimary setae, always few in number, also occur in fixed locations which are characteristic of some families. In most groups where they occur subprimary setae appear in later instars but in highly specialized families such as the Lycaenidae they occur in the first instar. Secondary setae, which are numerous in some families, are variable in number and position, generally most abundant in the last instar, and only rarely occur in first instars.

For most (perhaps all) lycaenids the distribution pattern of primary and subprimary setae is obscured by numerous secondary setae in instars following the first. Among the fauna included in this survey there are several structurally distinct types of secondary setae whose size, number, and distribution are often taxonomically useful.

The basic setal structure consists of a hollow shaft (usually with lateral processes or spiculations) arising from a basal ring which surmounts a short sclerotized prominence or chalaza. In the Lycaenidae variations in setal structure range from long, slender, and finely tapered to short, stout, and capitate while their lateral processes range from long slender filaments to short, stout, pointed dentations and minute granulations. In some taxa setal structure is nearly uniform regardless of setal size or location but more often the longest setae are most erect and most tapered while the shortest setae are most curved and/or clavate. The longest setae also tend to be in locations where true primary setae are expected to occur (i.e. dorsal, subdorsal, lateral, etc.). Often there is a gradient in setal structure with the most clavate, capitate, or recurved setae occurring dorsally on A7-A10. Setae with the longest lateral processes (relative to setal length) occur most frequently in close proximity to the honey gland and spiracles.

In the known larvae of New World riodinines most setae are gradually tapered, filamentous, or short and multibranched while strongly bent setae are absent or rare. Also, the longest setae (often much longer than the head width) arise from the prothoracic shield and/or dorsal and laterval verrucae. But in the Old World *Z. flegyas* setal structure is often more complex and those setae on the prothoracic shield barely reach the posterior cranial margin. In *Calephelis* the longest setae may be longer than the body width while the shortest setae, which occur densely over the dorsal and lateral regions, are too small to be individually discerned without magnification. In *Apodemia* all body setae are gradually tapered or filamentous and those arising from verrucae are primarily stiff and spinelike.

For the purpose of describing the larvae treated in this survey seven common categories of setae are defined: 1) **prominent** (figs. 2a, 4), 2) **dendritic** (figs. 2p, 15-18), 3) **sensory** (figs. 6, 9-14), 4) **neck** (fig. 27), 5) **mushroom** (figs. 2q, 22), 6) **plumose** (figs. 31, 32), and 7) **echinoid** (fig. 31). Prominent and sensory setae occur in all lycaenid subfamilies represented in California but dendritic and neck satae are absent in the

Riodininae, mushroom setae occur only in the Lycaeninae, and plumose and echinoid setae occur only in the Riodininae. The first four setal categories are widespread in the Lycaenidae; the last three may occur only in relatively small groups (subfamily, tribe, etc.) and it is likely that other structurally equivalent setal categories could be defined for other small phyletic groups. However, the majority of larval setae do not fit the categories enumerated above; they comprise an unnamed assemblage of perhaps less specialized setae with diverse structures (figs. 2b-2o).

Prominent setae of Lycaenidae occur in specific locations which coincide with sites where true primary setae are found in most other Lepidoptera. However, the number of prominent setae in a given location is variable and often exceeds the basic number of primary setae; they may also be absent. They are always cylindric, tapered, erect, and straight to gently curved (figs. 2a, 4); in many species they differ from surrounding setae only in their much greater length. This setal category corresponds to the major setae of Lawrence and Downey (1966), Downey and Allyn (1979), and Wright (1983). Prominent setae on the prothorax usually occur abundantly along the anterior and lateral margins where they can serve as the anterior most tactile receptors when the head is withdrawn. Additional prominent setae may occur on the prothoracic shield or near its anterior and posterolateral margins. On all other segments prominent setae occur singly or in groups dorsally (flanking the middorsal line), subdorsally (about half way between the spiracles and middorsal line), and laterally (below the spiracles, along the lateral fold) (fig. 1). Aside from the prothorax, prominent setae tend to be most abundant on the mesothorax and progressively less abundant posteriorly, although there is usually little difference in their numbers on A1-A6. In species having a honey gland there are no dorsal prominent setae on A7. Subdorsal prominent setae are least encountered but usually occur on T2 and are more likely to occur on A6 and A7 than on A1-A5. Lateral prominent setae usually occur on all segments but are reduced or lacking in some species. Prominent setae are almost always present along the anterior and lateral margins of the prothorax and posterolaterally on A10. In the California riodinines most prominent setae occur on verrucae and the prothoracic shield. In *Apodemia* they are primarily stiff and spinelike but in *Calephelis* they are mostly long, slender, and plumose. These latter setae are morphologically distinctive enough to be accorded a separate setal category (plumose setae) discussed below.

Dendritic setae can be distinguished from other secondary setae by structure and location. They may appear tree-like due to the presence of filamentous lateral processes arising from the apical half which are usually longer than the setal width at their point of origin. These setae are weakly tapered to clavate, erect, straight (rarely slightly curved), and less pigmented than other setae. They are usually restricted to a few

locations (where lenticles may also be concentrated) such as the margin
of the honey gland and spiracles, but are more widespread in some taxa
and absent in others. Commonly at least a pair of dendritic setae occurs
at each lateral angle of the honey gland where they may be obscured if
the gland opening is retracted. The dendritic appearance of these setae
varies due to the relative length of their lateral processes. Although the
processes are usually much longer than the setal width (figs. 15-17),
they can be shorter and may not be easily seen (especially those at the
lateral angles of the honey gland) (fig. 18). In such cases dendritic setae
can usually be distinguished by their greater prominence (surrounding
nondendritic setae are often shorter and clavate-capitate or recurved).
Lawrence and Downey (1966) used the terms spiculate and dendritic for
this type of setae on the larva of *E. comyntas* and likened their
appearance to Christmas trees. Other terms for dendritic setae which
appear in the literature include spiculate and hydroid setae (Downey
and Allyn, 1979) and branched hairs (Kitching, 1983).

The function of dendritic setae is not well established but there are
indications that they may be involved in chemical and/or tactile
communication with ants. Our observations indicate a direct relation-
ship between the abundance of these setae and the degree of ant-larval
association (research in progress). Thus, while larvae of all twelve
California species of Lycaeninae lack the more notable ant association
organs (honey gland and eversible tubercles), the four which have
dendritic setae are the only ones which we have found associated with
ants.

Although all setae may have a sensory function, the term sensory
setae has been applied to a unique pair of setae on the lycaenid
prothoracic shield (Downey and Allyn, 1979 and 1984). They have also
been termed XD2 (*op. cit.* and Wright, 1983) and major setae 'type a'
(Lawrence and Downey, 1966). But setae of homologous structure found
in other Papilionoidea and at least some Arctiidae, Geometridae,
Saturniidae, and Sphingidae occur anterior and/or anterodorsal to the
T1 spiracles and often subdorsally on other segments; their location
coincides with Hinton's SD1 setae. These are the only primary body setae
which can be recognized in all lycaenid instars. They occur in all
California lycaenids and in nearly all exotic species examined; none
were found in the liphyrine *L. brassolis* nor in the miletines *F.
tarquinius* and *S. epeus*. The function of the sensory setae is unknown
and they are curiously insensitive to tactile stimulation.

The structure of the sensory setae varies among different taxa. They
may be filiform, flagelliform (fig. 14), clavate (fig. 12), spatulate (fig. 13),
or even branched (fig. 6). In most species the sensory setae have
inconspicuous lateral spicules but in others the spicules are longer,
causing the sensory setae to appear brush-like (fig. 9). In the Lycaeninae
the lateral spicules are confined to the apex (best seen with SEM) or
absent (fig. 14). Sensory setae are more slender, at least basally, often

longer, and more flexible than other setae on the prothoracic shield; they arise from uniquely low, button-like chalazae. In live larvae their flexibility and fine basal attachment result in a vibratory or slow twitching motion in weak air currents which may cause them to appear independently motile.

Mushroom setae are known to occur only in members of the Lycaeninae (Wright, 1983). Malicky (1969) referred to this type of seta as Baumchenhaare (tree setae) in his treatment of the European *Lycaena* species. Under low magnification they appear as short, rounded structures resembling mushrooms but with higher magnification they can be seen to have numerous short, stout distal and lateral processes (figs. 2q, 22). They are usually nonpigmented and much shorter than other setae among which they are scattered over the dorsal and lateral body surfaces. To the unaided eye they may appear as minute white speckles in contrast to the darker larval ground color. Structural variations in the mushroom setae, especially their lateral processes, may be useful taxonomic characters (figs. 2q and 22) but since these cannot be seen without SEM they are of little use in larval identification.

The lycaenid larval neck can be densely covered with minute setae and/or spinules which give it a granular appearance. These neck setae typically are much shorter than other secondary setae, stout (often tooth-like), may be rounded or acute apically, and may have a few short, stout apical or subapical spicules (fig. 27). Spinules are shorter than neck setae and range from pointed to rounded and may be erect or recumbent (figs. 27, 28). Both neck setae and spinules are apparent on the posterior half of the neck where their distribution usually ends abruptly at the junction with the nonretractable remainder of the prothorax. In some lycaenines and theclines neck setae are also sparsely scattered dorsally and laterally over the remainder of the prothorax. Under the dissecting microscope it may be difficult to discern whether they are setae (with supporting chalazae) or merely spinules. In the Theclinae and Lycaeninae both neck setae and spinules are abundant on the posterior half of the neck. In the Polyommatinae there is a narrow dorsal band of spinules at the posterior end of the neck and a more extensive ventral patch of spinules and neck setae anterior to the prothoracic legs. Neck setae and spinules were not observed in the Liphyrinae, Miletinae, and Riodininae. Although differences in the structures of the neck setae and spinules may provide characters for taxonomic studies they are difficult to observe without SEM and are not discussed further here.

Plumose setae occur only in the riodinines and are most apparent on the prothoracic shield and verrucae. They are slender filaments densely clothed with short, fine lateral processes which may confer a velvety appearance (figs. 31, 32). These setae are mostly uniform in width throughout most of their length but may be apically spatulate (fig. 32) or abruptly tapered. In *A. mormo* a single plumose seta may arise from

each dorsal verruca and 4 or more from each lateral verruca along with numerous shorter spine-like setae (fig. 69), but in *Calephelis* the verrucae are comprised entirely of plumose setae (fig. 70). In the latter genus these setae vary greatly in length but many are longer than the body width and confer to a larva the appearance of a down feather; much shorter plumose setae occur primarily near the verrucae, on the prothoracic shield, and near the intersegmental lines. Also in *Calephelis* a few plumose setae on dorsal verrucae are relatively short, stout, and somewhat spatulate.

Echinoid setae were found only in *Calephelis* larvae. Due to their small size and density they may cause the body surface to appear pollinose or mealy. They are rather short and stout and adorned with relatively large lateral processes which taper from broad bases but are apically flared (fig. 31). Other authors have referred to these setae as many-pointed branching stars in *C. wrighti* (Comstock, 1928), stellate nodules in *C. nemesis* (Comstock and Dammers, 1932), silvery stars in *C. borealis* (Grote and Robinson) (Dos Passos, 1936), and sprocket-shaped processes in *C. muticum* McAlpine (McAlpine, 1938).

Other secondary setae span a wide range of structural forms including erect, recumbent, straight, recurved, tapered, and clavate-capitate (figs. 2b-2o). In some species these setae are uniform in structure but commonly there is a structural gradient with the most extreme forms occurring in specific areas. The most recurved and clavate or capitate setae usually occur dorsally on abdominal segments 7-10 (especially near the honey gland). The nearly continuous range of structural variation in these setae among different species and even on individual larvae diminishes the value of defining specific structural types for them.

All setae on the larval body normally arise from sclerotized tubercles or **chalazae**. Ventral chalazae are typically cylindric but dorsal and lateral chalazae may be sculptured in the Polyommatinae and Theclinae. The chalazae of most species of Polyommatinae appear stellate or crown-like due to conspicuous lateral or distolateral points (figs. 2e, 2f, 2j, 2k, 13, 16). In the Theclinae the chalazae are most often conical with longitudinal ridges resembling buttresses which are most prominent basally where they fuse with the cuticle (figs. 2n, 2o, 4); similar chalazae occur in the Curetinae (DeVries, et al, 1986). In the liphyrine *L. brassolis* the dorsum is covered with highly modified flattened, shingled chalazae bearing much smaller setae; toward the ventral margin of the dorsal carapace these chalazae become more erect and cylindric and appear somewhat stellate. In all Lycaeninae, Miletinae, and Riodininae examined the chalazae are smoothly contoured and cylindric or globular (figs. 2i, 15). Although the structural distinctions between the chalazae of the Polyommatinae and Theclinae are true for most species examined, there are some exceptions. In the polyommatines *P. emigdionis* from California and *C. xanthospilos* from Australia, the chalazae appear

buttressed rather than stellate. In the former species SEM photographs show that the lateral ridges are not distobasally fused with the cuticular surface (fig. 10) but in the latter they are very similar to typical thecline chalazae. Larvae of the Arizona thecline, *Erora quaderna*, have stellate chalazae much like those of the Polyommatinae. Also, some members of both subfamilies have apparently nonsculptured chalazae as in the Lycaeninae.

In many lycaenids the degree of sculpturing of the chalazae varies for different types of setae and in different body regions. The most sculptured and strongly pigmented chalazae often occur on or near the prothoracic shield. Chalazae associated with dendritic setae are usually less sculptured than those of other setae and may appear nonsculptured. In the Polyommatinae the chalazae of prominent setae tend to be larger but less stellate than those of shorter adjacent setae. The chalazae associated with neck setae and the sensory setae on the prothoracic shield are not sculptured. The latter are visibly low and button-like (figs. 6, 9, 11, 12, 14) in the Lycaeninae, Theclinae, and Riodininae whereas in the Polyommatinae they are often slightly sunken below the cuticular surface (figs. 10, 13). Their visible dorsal surface is glassy smooth and flat or convex, much like a lenticle with a small central pore from which the sensory seta emerges.

Lenticles are small lens-like cuticular structures often resembling chalazae without setae; they may be present in all lycaenids and thus constitute an important diagnostic character. Other terms for lenticles include perforated cupolas (Malicky, 1970), Allyn's organs (Downey and Allyn, 1979), and pore cupolas (Kitching and Luke, 1985). Malicky (1970) found them in 60 species of (primarily European) lycaenids. In this study they were found in all lycaenid species examined except *L. brassolis*. The larval dorsum in that aberrant species is densely covered with overlapping chalazae; but there are regularly placed pores which may lead to recessed glands and/or lenticles, as suggested by observations of the inner surface of larval exuviae (Bethune-Baker, 1925).

Lenticles have a low, round, convex or flat central region surrounded by a narrow collar; the latter may be smoothly rounded and cylindric, buttressed, or stellate much like the chalazae of nearby setae (figs. 15, 16, 17, 19). Although the lenticles of first instar larvae are few in number and occur in fixed locations, those of later instars are more numerous, variable in number, and more randomly distributed. In mature larvae lenticles tend to be sparsely scattered over dorsal and lateral body regions but more numerous near the honey gland and spiracles (especially on A8).

The function(s) of the lenticles remains somewhat speculative but at least some seem to be related to myrmecophily. Malicky (1970) suggested that lenticles have a chemical communication function since they are most abundant in areas commonly attended by ants and at least some have a porous surface and are associated with epidermal glands.

Lenticles of similar structure occur in hesperiid larvae (which are not myrmecophilous) where they have been shown to be formed by cells which can also produce setae (Franzl et al, 1984). Henning (1983b) found in some South African lycaenids that the body surface containing lenticles also contains a chemical which mimics an associated ant's brood pheromone.

A specialized type of lenticle, found in *A. halesus*, has a mushroom shape. **Mushroom lenticles** differ from other lenticles primarily in being stalked or elevated above the body surface and narrowest at the base; also, the collar surrounding the central lens is relatively broad and divided into radial segments by narrow ridges (figs. 6, 26). Under low magnification these lenticles appear similar in size and form to the mushroom setae of *Lycaena* larvae and, likewise, confer a minutely white speckled appearance to the larva. They are randomly distributed over the dorsal and lateral body regions but replaced by more ordinary appearing lenticles on the prothoracic shield and areas adjacent to the spiracles and honey gland.

The presence of a pair of **eversible tubercles** (tentacular organs) dorsolaterally on abdominal segment eight is a common trait in the Lycaenidae; they have been reported in the subfamilies Curetinae, Liphyrinae, Polyommatinae, and Theclinae (Cottrell, 1984). The appearance of these organs differs little among the California species. Ordinarily they are retracted into the body but when everted they can be seen (in most species) to have an apical cluster of relatively long, straight, prominently spiculate setae (fig. 20). The spicules on these setae are slender and rather evenly distributed whereas those of dendritic setae, which they otherwise resemble, are concentrated in the apical half of the seta. In some exotic taxa variations in the structure of the tubercles and in the number, size, and color of their terminal setae are of taxonomic value (Clark and Dickson, 1956a); the eversible tubercles of some exotic species such as *Ogyris genoveva* and *Candalides xanthospilos* lack setae.

Among the California fauna eversible tubercles are absent in the Lycaeninae, Riodininae, and Theclinae but well developed in all Polyommatinae except *A. franklinii* and *P. speciosa*; they may be nonfunctional in some populations of *E. amyntula*. Generally these organs are everted briefly at irregular intervals or in response to tactile stimuli but in some, such as *P. emigdionis*, they pulsate regularly and are frequently everted as the larva crawls. The function of the tubercles may vary among different taxa; Clark and Dickson (1956a) felt that 'whip' type eversible tubercles in Aphnaeini mechanically remove bothersome ants; some other authors (Henning, 1983a and b; De Vries, 1984; Kitching and Luke, 1985) suggest that the tubercles in other taxa release a chemical which mimics an ant alarm pheromone. In preserved larvae they are seldom everted, but their locations usually can be discerned by the presence of a small circle of setae surrounding a bare

wrinkled depression (which may surmount a low prominence) slightly
posterolateral to the eighth abdominal spiracles.

The **honey gland** (Newcomer's organ or dorsal nectary organ) is a
feature present in many species of Polyommatinae and Theclinae but
apparently absent from other lycaenid subfamilies. It usually appears
as a narrow transverse middorsal furrow on A7; in the exotic *H. erylus*
the honey gland occurs on the eighth abdominal segment, closely
flanked by the spiracles. In response to stimulation by ants the gland
can partly evert (fig. 19) and discharge a drop of fluid which ants imbibe.
For some species this fluid has been shown to contain both sugars and
amino acids (Maschwitz et al, 1975; Pierce, 1983). In discussing the
relationship between ants and lycaenid larvae, Malicky (1969, 1970)
suggested that the honey gland provides a bribe to forestall aggression
by ants. Pierce and Mead (1981) noted that ant-tended larvae of *G.
lygdamus* were significantly less parasitized than untended larvae and
suggested that the honey gland attracts ants which defend the larva
much as they do other nectar sources. Henning (1983b) minimized the
importance of the honey gland and suggested that chemicals produced
by other organs (chiefly lenticles) were responsible for maintaining a
benign (even protective) attitude by ants toward lycaenid larvae. A
honey gland is not necessary for attracting ants since mymecophily
occurs in some taxa, such as *Lycaena*, which have no honey gland.
Among California lycaenids the honey gland is absent in the Lycaeninae
and Riodininae, but present in all Polyommatinae except *A. franklinii*
and in all Theclinae except *H. grunus*. The external gland opening is
usually surrounded by numerous lenticles and often by dendritic setae
as well. In some exotic species the base of the gland and/or the
surrounding cuticle is strongly sclerotized, but in the local fauna little
or no sclerotization is apparent. Although the surrounding setae may
provide useful diagnostic characters, the appearance of the honey gland
itself is of little use in discriminating the local fauna.

The arrangement of the **crochets** and presence of a **spatulate lobe** on
the prolegs are good characters for distinguishing most lycaenids.
Typically in this family there is a well developed bi- or triordinal
mesoseries of crochets which may be weakened or divided medially by a
fleshy lobe (fig. 72). Many taxa also have a less well developed lateral
series of crochets; in *L. brassolis* it is so well developed that an
essentially complete ring of crochets is apparent. In the California
fauna a lateroseries of crochets occurs in the Riodininae (except *A.
mormo*), in the Lycaeninae (sometimes greatly reduced or absent on
some prolegs) and in *H. grunus* (fig. 72a). The fleshy lobe which often
divides the mesoseries of crochets is strongly spatulate in most species
but absent in both *A. mormo* and *P. emigdionis*.

Cephalic pigmentation is a useful diagnostic character for several
taxa. In most California Polyommatinae the cranium is uniformly dark
brown or blackish but in the Lycaeninae and Theclinae it is often

yellowish. The cranium is usually dark in *A. mormo* but pale or nonpigmented in the other three riodinine species. A narrow band of dark pigment is usually associated with ocelli (stemmata) 1-5 (fig. 45); ocelli are numbered as in fig. 68. One should not confuse this cuticular infuscation with the subcuticular ocellar pigment which is often visible in preserved specimens. A few local and many exotic polyommatine species have light brown head color while some lycaenine and thecline species have extensive dark cranial infuscation.

Cephalic setation is a relatively conservative trait in most lycaenid groups. Cranial setae are usually few in number and very small (fig. 3) except for those near the oral margin. More numerous short setae (similar to neck setae) may occur, especially in the Lycaeninae and Theclinae, on the frons (fig. 29) and ventral to the ocelli. The cranial secondary setae of the Riodininae are more numerous and may be as long as some prominent setae on the body (fig. 5).

The number of **mandibular setae** may be variable but is useful in distinguishing some taxonomic groups. This character was examined for only a limited number of specimens of each species. Although it has been reported that riodinines have more than two mandibular setae while other lycaenids have only two (Scott, 1986; Downey, 1987; Harvey, 1987), there are numerous exceptions. In this study two mandibular setae were found in all polyommatines, most theclines (fig. 55a), and in the Southeast Asian riodinine, *Z. flegyas*. But some theclines have as many as six mandibular setae, while two to five were found in the Lycaeninae (fig. 55b); 24 mandibular setae were found in the riodinine *M. pixe*. *Spalgis epeus* has one madibular seta.

There are notable differences in the **prothoracic shield** among the California taxa surveyed here. In the riodinines the shield is transverse, rather strongly sclerotized, and adorned with numerous long setae which overhang the head. In the other lycaenids the shield is about as long as it is wide (sometimes longer), variably sclerotized, somewhat recessed below the level of the surrounding cuticle (figs. 1, 21), and has setae which seldom extend much beyond its anterior margin. In the Lycaeninae, Riodininae, and Theclinae the surface of the prothoracic shield usually appears smooth (figs. 9, 11, 12, 14, 21). In polyommatines the surface of the shield appears (in SEMs) honeycombed with a complex ultrastructure of anastomozing ridges similar to, but more highly developed than, those elsewhere on the body (figs. 10, 13); this surface also occurs on the prothoracic shield of some theclinae such as *A. halesus* (fig. 6).

Body coloration is highly variable in the Lycaenidae since most species are cryptically colored to match their substrate. The predominant ground color is green but pink, white, yellow, and brown are also common. Except in the riodininae a disruptive pattern of contrasting lines is often present. The latter may appear complex but usually can be reduced to a few standard components.

The following color pattern components are recognized: 1) **middorsal line**, 2) **subdorsal lines**, 3) **lateral lines**, 4) **lateral chevrons**, 5) **transverse bar**. The first three are longitudinal and generally extend posteriorly from T2 or T3. The lateral chevrons extend posterolaterally from the subdorsal area of one segment to near the lateral line on the second segment behind it. These may appear as a series of parallel diagonal lines or chevrons when the larva is viewed from above. In some taxa there is a transverse bar of dark pigment on the first abdominal segment. The transverse bar is always darker than the ground color and is commonly reddish or brown; it varies in extent from a pair of unconnected and relatively small dark dorsal spots, as in *C. (C.) dumetorum, C. (I.) augustus*, and *C. (M.) spinetorum* (figs. 74-4b, -4d, -5c), to a broad band extending across the dorsum toward the lateral line, as in *E. rita* (fig. 74-8d). Variations in this basic pattern of lines result from two factors: 1) each line may be highlighted dorsally and/or ventrally by lines of contrastingly darker or lighter pigment and 2) the degree to which each line and its bordering pigment are developed may vary independently on each segment. Some or all lines may be absent or reduced to discontinuous spots on some or all segments. Monophagous and oligophagous species are usually mono- or oligomorphic while polyphagous species are often polymorphic. These color pattern components (except the transverse bar on A1) are illustrated in figure 1.

KEY TO LAST INSTAR LYCAENIDAE OF CALIFORNIA

1.   The most conspicuous body setae clustered on verrucae; some setae on prothoracic shield extending anteriorly over head; A1 spiracles displaced ventrally to a location slightly anteroventral to the lateral verrucae (figs. 30, 69, 70); head not retractable. (Riodininae)   2.

1′   Body setae not arranged in verrucae; no setae on prothoracic shield extending beyond anterior margin of prothorax; spiracles on first abdominal segment in line with those on other abdominal segments (fig. 1); head retractable. . .   5.

2(1)   Segments A1-A7 each with 2 pairs of dorsal verrucae consisting of numerous fine, flexible plumose setae many of which are longer than twice the head width (fig. 70); subdorsal verrucae absent; dorsal and lateral body regions densely covered with echinoid setae (fig. 31). . .   3.

2′   Segments A1-A7 each with 1 pair of dorsal verrucae consisting mostly or entirely of short spine-like setae (fig. 30); subdorsal verrucae present on segments T2-A7 (fig. 69); echinoid setae absent. . .   4.

3(2)   Some plumose setae on verrucae apically spatulate (figs. 32, 70); hosts *Baccharis glutinosa* and *Encelia californica*. . .   *Calephelis nemesis.*

3′   Verrucae lacking apically spatulate setae; host *Bebbia juncea*. . .
                                                         Calephelis wrighti.

4(2′)   Dorsal verrucae with darkly pigmented setae; dorsal verrucae on segments A1-A7 (in most populations) also with one nonpigmented plumose setae ca 3X as long as other verrucal setae (fig. 69); hosts *Eriogonum, Krameria,* and *Oxytheca*. . .   *Apodemia mormo*

4′   All setae on dorsal verrucae on segments A1-A7 nonpigmented, spinelike; host *Prosopis*. . .   *Apodemia palmerii.*

5(1′)   Eversible tubercles present on A8 (fig. 1) and/or chalazae stellate (figs. 2e, 2f, 2j, 2k, 16, 71) and/or head uniformly black or brown (may be darker around ocelli), ca 1/4 as wide as body; prothoracic shield not pigmented (apparently nonsclerotized). . .   (Polyommatinae) 45.

5′   Eversible tubercles absent; chalazae not stellate; head often yellowish or bicolored, ca 1/3 as wide as body; prothoracic shield sclerotized, often pigmented and acutely produced anteromedially. . .   6.

6(5′)   Honey gland absent; mushroom setae present on dorsal and lateral body regions (figs. 21-24); prothoracic shield lacking setae lateral to sensory setae (figs. 21, 33-44); chalazae nonsculptured (figs. 2i, 2p). . .
                                                (Lycaeninae) 7.

6′   Honey gland present on A7 and/or chalazae buttressed (figs. 2n, 2o, 4); mushroom setae absent; prothoracic shield with some setae lateral to sensory setae (figs. 45-54, 61, 64, 67)   (Theclinae) 18.

7(3)   Prominent setae absent on T2-A9; nearly all setae ca as long as spiracle width, recumbent, truncate; sensory setae often apically truncate-spatulate, at least 3X as long as dorsal setae on T2-A9 (fig.

21); host *Rhamnus crocea* in San Diego Co. and northern Baja California...   *Lycaena hermes.*

7'   At least some dorsal setae much longer than spiracle width and/or erect; sensory setae not apically truncate-spatulate, seldom longer than all dorsal setae on T2-A9; host not *Rhamnus crocea*; more widely distributed...   8.

8(7')   Nonprominent dorsal and lateral setae on T2-A6 nonpigmented, mostly ca 2X as long as spiracle width, recumbent, finely tapered (fig. 2i), often appearing whitish; host *Eriogonum*...   9.

8'   Nonprominent dorsal and lateral setae on T2-A6 more erect and/or brownish, shorter, and not finely tapered; host not *Eriogonum*...   10.

9(8)   Distinct dorsal prominent setae present on T2-A8; some setae near spiracles on A8 erect, straight and weakly dendritic (fig. 2p)...
                                                                Lycaena heteronea.

9'   Dorsal prominent setae absent or indistinct on T2-A8; setae near spiracles on A8 rarely erect and straight, never dendritic...
                                                                Lycaena gorgon.

10(8') Dendritic and short clavate-capitate setae present subdorsally and near spiracles on A7, A8 (fig. 15)   11.

10'   No dendritic or clavate-capitate setae subdorsally or near spiracles on A7, A8; on various hosts...   13.

11(10) Head light brown but may be darker anteriorly (fig. 44); legs light brown to nonpigmented; widely distributed mostly below 2000m ...
                                                                Lycaena xanthoides.

11'   Head dark brown, evenly pigmented throughout (figs. 42, 43); legs dark brown; usually found above 2000m in central and northern California...   12.

12(11') Dorsal and lateral prominent setae on T2-A8 ca 4X as long a spiracles; no more than 25 secondary setae on prothoracic shield, most of which are mushroom setae and the remainder are apically rounded (fig. 42)
        ...   *Lycaena editha.*

12'   Dorsal and lateral prominent setae on segments T2-A8 ca 3X as long as spiracles; at least 30 secondary setae on prothoracic shield of which less than half are mushroom setae and the remainder are mostly tapered (fig. 43)...   *Lycaena rubidus.*

13(10') Head and legs predominantly dark brown (figs. 33, 34); all body setae erect or nearly so, never strongly bent parallel to body surface; alpine species usually found above 3000m; hosts *Oxyria* and *Rumex*...   14.

13'   Legs yellowish or nonpigmented; head yellowish at least near vertex (may be dark anteroventrally); some body setae may be strongly bent nearly parallel to body surface; seldom found above 3000m; on various hosts...   15.

14(13) Dorsal and lateral setae on T2-A8 shorter than sensory setae on prothoracic shield, ca as long as spiracle width...   *Lycaena cupreus.*

14′   At least some dorsal and lateral setae on T2-A8 longer than sensory setae on prothoracic shield, ca 2X as long as spiracle width...

                                          Lycaena phlaeas.

15(13′) Longest dorsal prominent setae on T1 posterolateral to prothoracic shield at most subequal to length of sensory setae; nonprominent setae in same area bent caudad (fig. 23); all or most nonmushroom setae tapered, apically pointed, erect to suberect (fig. 23), rarely bent parallel to body surface; host *Ribes*...   *Lycaena arota.*

15′   Longest dorsal prominent setae on T1 posterior to prothoracic shield longer than sensory setae; nonprominent setae in same area bent cephalad (fig. 24); nonprominent lateral setae on T1-A9 often truncate and recurved or bent parallel to body surface; host not *Ribes*...   16.

16(15′) Most nonprominent setae near posterolateral margins of prothoracic shield bent nearly parallel to body surface (figs. 2c, 24); cephalic infuscation extending across frons and posteriorly well beyond ocelli (fig. 36); host *Polygonum douglassii* and perhaps other *Polygonum* and *Rumex* species...   *Lycaena nivalis.*

16′   Most nonprominent setae near posterolateral margins of prothoracic shield more erect, seldom bent at less than 45 degrees to body surface; cephalic infuscation less extensive (may be confined to ocelli 1-5); hosts *Polygonum, Rumex*, and Vaccinium...   17.

17(16′) Most nonprominent dorsal setae on T2-A8 tapered, acutely pointed, often bent nearly parallel to body surface; cephalic infuscation limited to an arc enclosing ocelli 1-5 (fig. 40); widely distributed; hosts *Polygonum* and *Rumex*...   *Lycaena helloides.*

17′   Most nonprominent dorsal setae on T2-A8 weakly tapered, truncate, less bent (ca 45 degrees to body plane) (fig. 2d); cephalic infuscation often more extensive (fig. 41); found in mountains of central and northern California; host *Vaccinium*...   *Lycaena mariposa.*

18(6′)   Honey gland absent; dorsal prominent setae present on A7; prolegs with a lateroseries of crochets (fig. 72a); prothoracic shield smoothly convex anteriorly and broadly rounded posterior to sensory setae (fig. 46); hosts *Chrysolepis chrysophylla, Lithocarpus densiflora*, and *Quercus chrysolepis*...   *Habrodais grunus.*

18′   Honey gland present; dorsal prominent setae absent on A7; prolegs lacking a lateroseries of crochets; prothoracic shield more-or-less 't'-shaped, often acutely produced anteromedially and abruptly narrowed posterior to sensory setae (figs. 45, 47-54, 61, 64, 67)...   19.

19(18′) All dorsal setae erect, straight, and tapered (figs. 7, 8) or recumbent and ca as long as their chalazal width (fig. 2n); sensory setae often with conspicuous lateral spicules (fig. 9)...   20.

19′   Some dorsal setae (at least on A8) clavate-capitate (fig. 2g), strongly bent, or recumbent (inclined caudad) and longer than their chalazal width; sensory setae lacking conspicuous lateral spicules (as in fig. 10)...   38.

20(19)   Mushroom lenticles (figs. 8, 26) widely distributed on dorsal and lateral body regions; dorsal prominent setae absent; prothoracic shield white, outlined with black (fig. 45); sensory setae 2-many branched (fig. 6); host *Phoradendron*...   *Atlides halesus.*

20'   Mushroom lenticles absent; dorsal prominent setae present or absent; prothoracic shield not white, outlined with black; sensory setae not branched; host not *Phoradendron*...   21.

21(20')   Sensory setae longer than all dorsal setae on T3 (fig. 73), often broadest in apical fourth (fig. 12); nonprominent dorsal setae shorter than or subequal to spiracle width; host *Arceuthobium*...   22.

21'   Sensory setae not longer than all dorsal setae on T3, not distinctly broadest in apical fourth; some dorsal setae on T3 at least 2X as long as spiracle width; not on *Arceuthobium*...   23.

22(21)   Sensory setae ca 10X as long as other setae on prothoracic shield and posterolateral to it on T1 (fig. 73); all or most dorsal setae on T2-A6 reclinate, ca half as long as spiracle width, subequal to chalazal width...   *Callophrys (M.) spinetorum.*

22'   Sensory setae ca 5X as long as other setae on prothoracic shield and subequal to longest setae posterolaterally adjacent to it; all dorsal setae on T2-A6 erect, mostly 1/2-1X as long as spiracle width and longer than their chalazal width...   *Callophrys (M.) johnsoni.*

23(21)   Dorsal prominences posterolateral to prothoracic shield well-developed, with longest setae randomly distributed over them (fig. 8); host Cupressaceae...   24.

23'   Dorsal prominences posterolateral to prothoracic shield poorly developed, with longest setae arranged more-or-less in a transverse line (fig. 7); host not Cupressaceae...   27.

24(23)   Hosts, *Juniperus california* and *J. osteosperma* from west end of San Bernardino Mts. west and north in inner Coast Ranges to central California, through Tehachapi Mts. to Walker Pass, and Mojave Desert and Great Basin mountain ranges; also associated with *J. occidentalis* from San Bernardino Mts. northward...
                    Callophrys (M.) siva.

24'   Using other hosts and/or found elsewhere...   25.

25(24')   Restricted to vicinity of Otay Mt. in San Diego Co.; host *Cupressus forbesi*...   *Callophrys (M.) thornei.*

25'   More widely distributed; host not *C. forbesi*...   26.

26(25')   Host *J. california* from Mexican border north to San Bernardino and Little San Bernardino Mts....   *Callophrys (M.) loki.*

26'   Hosts *Cupressus sargentii* and *Libocedrus decurrens* (also *J. california* rarely in inner coast ranges of central California)...
                    Callophrys (M.) nelsoni.

27(23')   Cranial infuscation limited to a narrow crescent connecting ocelli 1-5 and not extending to ocellus 6 (figs. 59, 61-64), or much more extensive across front and encompassing all ocelli (fig. 60)...   28.

27'   Cranial infuscation limited to ocellar area, connecting ocelli 1-5 and extending posteriorly to anterior margin of ocellus 6 but not broadly encompassing all ocelli (figs. 65-67)...   35.

28(27')   Cephalic infuscation limited to a narrow band connecting ocelli I-V; host not *Eriogonum* or *Lotus*...   29.
28'   Cephalic infuscation variable; host *Eriogonum* or *Lotus*...   32.

29(28)   Frons slightly darker than remainder of head (fig. 64); host *Sedum*...
                                                        Callophrys (I.) mossii.
29'   Fronto-clypeal area not darker than remainder of head; host not *Sedum*...   30.

30(29')   Head width greater than 1.5mm; longest dorsal setae on T2 ca 1.5X as long as sensory setae; host *Pinus*...   *Callophrys (I.) eryphon.*
30'   Head width less than 1.5mm; longest dorsal setae on T2 usually less than 1.3X as long as sensory setae; host not Pinus...   31.

31(30')   Ocellar infuscation forming a broad band connecting ocelli 1-5, extending anteriorly along margin of antennal insertion and posteriorly half the distance from ocellus 5 to ocellus 6 (fig. 63); host *Cowania mexicana* in mts. of central and eastern Mojave Desert...
                                                        Callophrys (I.) fotis.
31'   Ocellar infuscation less extensive, not extending anteriorly along margin of antennal insertion and posteriorly half the distance from ocellus 5 to ocellus 6 (fig. 62); absent from mts. of central and eastern Mojave Desert; host not *C. mexicana*...   *Callophrys (I.) augustus.*

32(28')   Usually below 1500m throughout cismontane California and the desert slopes bordering the western Mojave and Colorado deserts...
                                                        Callophrys (C.) perplexa.
32'   Found along central coast, in mountains of Mojave Desert, or above 2000m in Sierra Nevada northward...   33.

33(32')   Host *Eriogonum latifolium* (and occasionally *Lotus scoparius*) along coast from Monterey northward to Point Reyes...
                                                        Callophrys (C.) dumetorum.
33'   Not found along coast of central California; host other *Eriogonum* spp....   34.

34(33')   Found mostly above 2000m in the Sierra Nevada, Siskiyou, and Warner Mts....   *Callophrys (C.) lemberti.*
34'   Found in Mojave Desert mountains...   *Callophrys (C.) comstocki.*

35(27)   Body with a saw-toothed dorsal profile due to paired dorsal prominences on T3-A6 each with 1 (2 on T2) prominent seta ca 10X as long as spiracles and 3-10X as long as surrounding setae (fig. 56c); hosts *Acacia* and (primarily) *Prosopis*...   *Ministrymon leda.*
35'   Body lacking a saw-toothed dorsal profile; dorsal prominences on T2-A6 indistinct or absent; dorsal prominent setae on segments T2-A6 absent or poorly differentiated, no more than 5X as long as spiracles; on various hosts...   36.

36(35')   Chalazae milky, lighter than ground color (best seen in live larvae);
           host Malvaceae primarily in desert and mountains from San Bernar-
           dino Co. southwards...   *Strymon columella.*
36'   Chalazae not milky or noticeably lighter than ground color; many
           hosts but especially Fabaceae, Malvaceae, and Polygonaceae...   37.

37(36')   Restricted to Catalina Island; hosts *Lotus* and *Eriogonum*...
                                                          Strymon avalona.
37'   Widely distributed on many hosts...   *Strymon melinus.*

38(19')   Dendritic setae and clavate-capitate, apically truncate setae (fig. 2g)
           present dorsally on A7 and A8, and laterally on T1, T3, A1, and A7
           (between spiracles and margin of honey gland); host *Prunus vir-
           giniana*...   *Harkenclenus titus.*
38'   At least some dorsal setae on A7 and A8 recumbent, bent, or inclined
           caudad (fig. 2o), not clavate-capitate; distribution of dendritic setae
           variable...   39.

39(38')   Head dark brown (except along adfrontal sutures); dendritic setae on
           T1 lateral to prothoracic shield; all dorsal setae on T2-A6 erect,
           straight...   40.
39'   Head at least partly yellowish or light brown; no dendritic setae on T1
           lateral to prothoracic shield; dorsal setae on T2-A6 variable...   41.

40(39)   Legs dark brown; nondendritic dorsal setae on A7, A8 dark brown,
           acutely tapered, reclinate (nearly parallel to body surface) (fig. 2n);
           hosts *Ceanothus, Quercus*, and probably other woody perennials...
                                                          Satyrium californica.
40'   Legs nonpigmented; nondendritic dorsal setae on A7, A8 nonpig-
           mented, suberect, often inclined caudad at ca 45 degrees to the body
           plane, more-or-less clavate and apically rounded (fig. 2o); host
           Lupinus...   *Satyrium fuliginosum.*

41(39')   Prominent setae absent on A1-A6; dorsal setae mostly recumbent,
           broadest near middle, strongly dentate, (fig. 17); dendritic setae
           present subdorsally on segments T2, T3 (fig. 17); sensory setae at least
           3X as long as other setae on and posterolaterally adjacent to prothor-
           acic shield; host *Purshia*...   *Satyrium behrii.*
41'   Segments A1-A6 with some prominent setae and/or some dorsal setae
           erect, cylindric; dendritic setae absent subdorsally on segments T2,
           T3; sensory setae no more than 2X as long as other setae on and
           posterolaterally adjacent to prothoracic shield; host not *Purshia*...
                                                                           42.

42(41')   Prominent dorsal setae on segments T2-A6 erect, straight, orange-
           brown, forming a pair of dorsal bands each comprised of at least 18
           setae per segment (fig. 56a); sensory setae tapered; 2-4 dendritic setae
           present near sensory setae on prothoracic shield; host *Cercocarpus*...
                                                          Satyrium tetra.
42'   Prominent dorsal setae on T2-A6 less numerous (or absent), variable
           in pigmentation; sensory setae clavate to tapered; dendritic setae
           absent on prothoracic shield; host not *Cercocarpus*...   43.

43(42')   Cephalic infuscation limited to a narrow band enclosing ocelli 1-5 (fig. 50); dorsal prominent setae on segments T2-A6 erect, ca 3-4X as long as spiracles, host *Salix*...   *Satyrium sylvinus.*

43'   Cephalic infuscation extending across front and posterolaterally at least to ocellus 6 (figs. 49, 51); dorsal prominent setae on T2-A6 absent or 1-2X as long as spiracles; host not *Salix*...   44.

44(43')   Dorsal prominent setae inconspicuous, erect, ca 2X as long as spiracles and other dorsal setae (fig. 56b); all dorsal setae cylindric, orange-brown; sensory setae less than 2X as long as longest setae postero-laterally adjacent to prothoracic shield; host *Quercus*...
                                                                    Satyrium auretorum.

44'   Dorsal prominent setae absent or obscure; dorsal and lateral setae of two types: 1) erect, tapered, cylindric, and pale brownish and 2) recumbent, flattened (as in fig. 17), and nonpigmented; sensory setae ca 2X as long as longest setae posterolateral to prothoracic shield; host *Ceanothus*...   *Satyrium saepium.*

45(5)   Prominent setae only at anterior margin of prothorax; dorsal and lateral setae on T2-A6 recurved, clavate-capitate, ca as long as spiracles; sensory setae tapered; hosts Chenopodiaceae (especially *Atriplex* and *Chenopodium*) and *Sesuvium verrucosum* (Aizoaceae)...
                                                                    Brephidium exilis.

45'   At least a few prominent lateral setae on one or more of segments T2-A6 and/or sensory setae not tapered; dorsal and lateral setae on segments T2-A6 variable in structure; host not Chenopodiaceae (except *Atriplex canescens*) or *S. verrucosum*...   46.

46(45')   Sensory setae spatulate or apically broadened (fig. 13)...   47.
46'   Sensory setae finely tapered (fig. 10)...   53.

47(46)   Chalazae strongly stellate, lateral points often much longer than basal width of seta (fig. 2e); on various hosts...   48.
47'   Chalazae less stellate, lateral points (if present) seldom longer than basal width of seta (fig. 2j); hosts *Eriogonum* and *Oxytheca*...   49.

48(47)   Dorsal setae on T3-A6 erect to suberect or broadly recurved and finely tapered (fig. 2b), not sharply bent near base; dendritic setae only near honey gland; hosts Fabaceae and *Plumbago*...   *Leptotes marina.*
48'   Dorsal setae on T3-A6 recumbent, strongly bent near base (fig. 2f); dendritic setae near A1 spiracles and honey gland, and on prothoracic shield; many hosts but not *Plumbago*...   *Celastrina argiolus.*

49(47')   Eversible tubercles absent; chalazae not stellate; host *Eriogonum reniforme* or *Oxytheca*...   *Philotiella speciosa.*
49'   Eversible tubercles present; chalazae stellate; host various *Eriogonum* species...   50.

50(49')   Head dark blackish brown; legs much darker than body venter, nearly as dark as the head; dorsal prominences on T2-A6 well-defined, each with at least a pair of prominent setae directed posteromedially (fig.

57c); found in Great Basin mountain ranges, the east slope of the Sierra Nevada, and foothills bordering the Mojave Desert; hosts *Eriogonum davidsonii, E. deflexum, E. microthecum, E. plumatella, E. roseum, E. wrightii,* and perhaps *E. heermannii...*   *Euphilotes rita.*

50'   Head medium to dark brown; legs nonpigmented to light brown, not nearly as dark as head; dorsal prominences on T2-A6 moderately to weakly developed, with prominent setae directed more posteriorly (fig. 57b) or absent (fig. 57a); host various *Eriogonum* species...   51.

51(50')   At least two dorsal prominent setae on each of segments T2-A6 (fig. 57b); legs lightly pigmented; host *Eriogonum pusillum* or *E. reniforme* in the Mojave Desert from late winter to early summer...

Euphilotes mojave.

51'   Less than two dorsal prominent setae on each of segments T2-A6 and often none (fig. 57a); legs nonpigmented; host not *E. pusillum* or *E. reniforme*; widely distributed...   52.

52(51')   Host many species of *Eriogonum* but not *E. davidsonii, E. elongatum, E. latifolium, E. nudum,* or *E. wrightii...*   *Euphilotes battoides.*

52'   Host many species of *Eriogonum* but not *E. fasciculatum, E. heermannii, E. microthecum,* or *E. ovalifolium* (in California)...

Euphilotes enoptes.

53(46')   Honey gland and eversible tubercles absent; montane in northern and central California; host Primulaceae, especially *Dodecatheon...*

Agriades franklinii.

53'   Honey gland present; eversible tubercles present or at least a circle of setae marks the location where they should be; host not Primulaceae 23..   54.

54(53')   Prolegs lacking a spatulate lobe; segments T2-A6 often with a pair of dorsal prominent setae ca 10X as long as spiracle width; chalazae apparently buttressed (fig. 10); host *Atriplex canescens...*

Plebulina emigdionis.

54'   Prolegs with a spatulate lobe; setation variable; chalaze not apparently buttressed; host not *A. canescens...*   55.

55(54')   Dorsal setae on T2-A6 mostly erect, tapered to clavate or capitate, shorter than spiracle width; setae around honey gland capitate (fig. 25); host *Dudleya...*   *Philotes sonorensis.*

55'   Dorsal setae on T2-A6 variable but not clavate or capitate; setae around honey gland variable; host not *Dudleya...*   56.

56(55')   Lateral margins of spatulate lobes on prolegs pigmented, apparently sclerotized (fig. 72b)...   57.

56'   Spatulate lobes on prolegs nonpigmented, not apparently sclerotized...   58.

57(56')   Nondendritic dorsal setae on A7, A8 erect and straight, or weakly bent (as in Fig. 2j); usually in *Astragalus* seed pods...   *Everes amyntula.*

57'   Nondendritic dorsal setae on A7, A8 mostly moderately to strongly bent

(as in figs. 2c, 2k); host various herbaceous Fabaceae including *Astra-galus*, *Lotus*, and *Vicia*...   *Everes comyntas*.

58(56') Dendritic setae present laterally on A6-A8 and/or most subdorsal setae on T2-A6 erect, clavate-capitate (fig. 2j); legs nonpigmented, not darker than body venter; host herbaceous Fabaceae, especially *Astragalus*, *Lotus*, and *Lupinus*...   59.

58' Dendritic setae not present laterally on A6-A8; most subdorsal setae on T2-A6 not erect and clavate-capitate; leg pigmentation variable, may be darker than body venter; hosts *Eriogonum* and various Fabaceae... 60.

59(58) Prothoracic shield lacking prominent setae, the sensory setae at least 2X as long as other setae on the shield; most dorsal setae on A7, A8 (between spiracles) moderately to strongly bent (fig. 2k), not capitate; host *Lupinus*...   *Glaucopsyche piasus*.

59' Prominent setae usually present on prothoracic shield, the sensory setae often shorter than some other setae on the shield; dorsal setae on A7, A8 erect, mostly clavate-capitate (similar to fig. 2h) or bent apically (fig. 2j); not only on *Lupinus*...   *Lycaeides idas* and *L. melissa*.

60(58') Dendritic setae present near spiracles on A2; legs not darker than body venter; host *Astragalus*, *Lotus*, or *Lupinus*...   *Glaucopsyche lygdamus*.

60' Dendritic setae not present on A2; leg color variable; host *Eriogonum* or various Fabaceae...   61.

61(60') All dorsal setae on T2-A6 erect, straight; leg color variable; host not *Eriogonum*...   62.

61' Some dorsal setae on T2-A6 recurved or recumbent; legs not pigmented; host *Eriogonum* or Fabaceae...   64.

62(61) Legs nonpigmented, not darker than body venter; dorsal prominent setae in T2, T3 no more than 3X as long as other dorsal setae; widely distributed; host *Lupinus*...   *Icaricia icarioides*.

62' Legs brown, much darker than body venter; dorsal prominent setae on T2, T3 at least 4X as long as other dorsal setae; above 2000m in central and northern California; host not only *Lupinus*...   63.

63(62') Dendritic setae present in area between honey gland and spiracles on A7; chalazae on prothoracic shield much paler than legs; chalazae anterior to prothoracic shield with lateral points less than 1/4 as long as basal width of chalaza; host *Trifolium*...   *Plebejus saepiolus*.

63' Dendritic setae on A7 only at lateral margins of honey gland; chalazae on prothoracic shield as dark as legs; chalazae anterior to prothoracic shield with lateral points greater than 1/2 as long as basal width of chalaza; host prostrate *Astragalus* and *Lupinus*...   *Icaricia shasta*.

64(61') Dorsal setae on A8 and A9 and nondendritic setae near abdominal spiracles mostly bent parallel to body, broadest near middle, flattened in body plane, and pointed (as in fig. 2l)...   65.

64'   Dorsal setae on A8, A9 erect to strongly bent, cylindric, not broadest near middle, and mostly blunt (fig. 2m); nondendritic setae near abdominal spiracles gradually tapered to a blunt tip (as in fig. 2c)... *Icaricia acmon, I. lupini,* and *I. neurona.*

65(64) Longest dorsal prominent seta on T2 as long or slightly longer than longest seta on prothoracic shield; segments T3-A6 usually with at least 4 dorsal prominent setae (fig. 58b); no dendritic setae near spiracles on A1; hosts Fabaceae... *Hemiargus isola.*

65'   Longest dorsal prominent setae on T2 ca 2/3-3/4 as long as longest setae on prothoracic shield; segments T3-A6 usually with only 2 dorsal prominent setae (fig. 58a); dendritic setae present or absent near spiracles on A1; hosts *Eriogonum* and Fabaceae...

Hemiargus ceraunus.

DIAGNOSTIC SECTION

The larvae of the California lycaenids share several morphological traits which distinguish them from other families of Lepidoptera. These features have been discussed in some detail in the morphology section above. The presence of lenticles, a spatulate lobe on the prolegs, and an onisciform body shape typically separate the California lycaenids from other Lepidoptera larvae. These characters are not without exceptions: lenticles also occur in hesperiids, a spatulate lobe is present on some prolegs of some geometrid moth larvae while absent in two California lycaenids, and the Riodininae are only weakly onisciform.

Riodininae

Most riodinine larvae possess an unusual arrangement of spiracles. Those on the first abdominal segment are displaced anteroventrally far below the latitude of the other abdominal spiracles; they are located slightly anteroventral to the lateral verrucae (figs. 30, 69, 70) and are often hidden by an intersegmental fold.

Other characters which distinguish these larvae from other lycaenid larvae in California are a transverse prothoracic shield with some setae long enough to overhang the head and the most prominent body setae clustered in verrucae. The distribution of verrucae differs in the two genera represented.

The number of larval instars may be variable in all four California riodinines but the minimum (and usual) number for all populations examined is five. Both Dos Passos (1936) and McAlpine (1938) found 8-9 instars in *Calephelis borealis* and *C. muticum*, respectively. It is not certain whether true diapause occurs in any of the four California riodinines but partially grown larvae of *A. mormo*, *A. palmerii*, and *C. nemesis* were found on their host plants during winter. Larvae of *C. nemesis* were observed to feed briefly (ca one hour) in early afternoon each day during winter when the temperature exceeded 12.8 degrees C. before returning to habitual resting sites on dead foliage. Comstock (1930) also reported intermittent winter feeding behavior in larvae of *A. palmerii*. Some populations of *A. mormo* probably overwinter as ova.

Apodemia

There are two species of *Apodemia* in California. Their larvae have paired dorsal, subdorsal, and lateral verrucae on segments T2-A8 (fig. 69); the prothorax has paired subdorsal and lateral verrucae and a transverse shield which covers most of the dorsum. The verrucae and prothoracic shield primarily contain stiff straight (prominent) setae; these are dark brown in *A. mormo* but much lighter (often non-pigmented) in *A. palmerii*. Several plumose setae arise from each lateral verruca and the prothoracic shield, but are absent from the

subdorsal verrucae. In most populations of *A. mormo* a single plumose seta arises centrally from some or all dorsal verrucae (fig. 69) but these setae are absent from the dorsal verrucae of *A. palmerii*. Additional setae structurally similar to prominent setae on the verrucae, but somewhat smaller and paler, are scattered over the dorsal and lateral body surfaces of both species. Other distinguishing characters include a pale green or pinkish ground color and yellowish head for *A. palmerii* (fig. 74-1b) vs. a predominantly brown or violet-brown ground color (with yellow dorsal and dorsolateral verrucae) and usually brownish head for *A. mormo* (fig. 74-1a).

The most widely distributed species, *A. mormo*, feeds primarily on perennial species of *Eriogonum*, but ova have been collected (and larvae reared) on *Oxytheca perfoliata* (both Polygonaceae). *Krameria* (Krameriaceae) is a host of *A. mormo* in Texas (Kendall, 1976); it is also acceptable to locally collected *A. mormo*. Various populations of *A. mormo* occur throughout California. *Apodemia palmerii* occurs in the southern deserts and feeds on *Prosopis* (Fabaceae).

Calephelis

There are two species of *Calephelis* in California; *C. nemesis* occurs primarily in riparian situations in southern California, while *C. wrighti* occurs in xeric habitats in southern and eastern California. The larval hosts of the former species are *Baccharis glutinosa* and *Encelia californica* (Emmel and Emmel, 1973), while larvae of the latter feed on *Bebbia juncea*, all in the Asteraceae. The larval ground color of both species is cream or buff (fig. 74-1c). They have one pair of dorsal verrucae on T2, T3, and A8, but two pairs on A1-A7; subdorsal verrucae are absent, but a single pair of lateral verrucae occurs on T1-A8 (fig. 70). The verrucae consist mostly of very long, slender, nonpigmented or pale brown plumose setae which give the larva a feather-like appearance; similar setae occur on the prothoracic shield. There are no straight, stiff, spine-like setae as in *Apodemia* but echinoid setae (fig. 31) cover most of the lateral body areas. The head is yellowish with a small amount of brownish mottling. In *C. nemesis* many plumose setae (ca 1/4-1/2 as long as the longest ones) on each verruca are broadly spatulate apically (figs. 32, 70), while in *C. wrighti* no spatulate setae occur. In both species a few short, clavate, plumose setae are present on the dorsal verrucae and often near the spiracles. These are mostly nonpigmented, but those on the dorsal verrucae on segments A1 and A7 are often black (especially in *C. wrighti*).

Lycaeninae

The Lycaeninae is one of the smallest yet widely distributed lycaenid subfamilies and may be better represented in California (twelve species) than in any other region of equivalent size. Most local species are

univoltine, diapause as ova, and use host plants in the Polygonaceae. For many years these were placed in the genus *Lycaena*, but Miller and Brown (1979) divide them among six genera. On the basis of similar biology and/or morphology of immature stages, it is convenient to discuss them as five groups which do not coincide with the generic arrangement of Miller and Brown (1979). Pending further comparative studies, we retain the single genus *Lycaena* for the group.

Lycaena

The larvae of all members of this genus lack a honey gland and eversible tubercles. The length of the prothoracic shield is about twice as great as its width. It is acutely pointed at the anterior, posterior, and lateral extremities and is generally diamond-or 't'-shaped (figs. 33-44). Although the width is greatest along the line of the sensory setae (in the anterior third), there is typically a second lateral expansion in the posterior third. Prominent setae are absent from the prothoracic shield; other secondary setae on it are much shorter than the sensory setae and never occur lateral to them. The sensory setae usually appear finely tapered and devoid of lateral spicules; but minute lateral spicules (visible with SEM) may occur near the apex in some species such as *L. mariposa*. Mushroom setae, which are unique to this group, are scattered over the dorsal and lateral body regions. Although mushroom setae may occur as early as the second instar, they are more likely to appear first in the third or fourth instar. Dendritic setae are present only in *Lycaena editha, L. heteronea, L. rubidus*, and *L. xanthoides*. The chalazae of all setae are nonsculptured or very weakly buttressed. Typically, a latero-series of crochets (in addition to the mesoseries) occurs on the prolegs but it may be greatly reduced or absent on some prolegs. *Lycaena editha, L. rubidus*, and *L. xanthoides* typically have three mandibular setae (*L. xanthoides* rarely has up to five) while the other *Lycaena* species typically have two mandibular setae. But in some populations of *L. gorgon* and *L. heteronea* there may be three mandibular setae.

Two species which differ similarly in larval morphology and biology from the others are *L. cupreus* and *L. phlaeas*. In California both occur mostly above 3000m, are univoltine, and typically have four larval instars; *L. phlaeas* sometimes has five instars. Both species probably diapause as larvae. When reared from ova in the lab at 25-27 degrees C. some larvae of *L. cupreus* often complete development but most enter diapause in the third instar. Under the same conditions *L. phlaeas* is continously brooded. In nature mature larvae of both species were found in mid-July and younger larvae in August. In California the larvae of *L. cupreus* are associated with *Rumex*, especially *R. paucifolius*, and larvae of *L. phlaeas* are associated with *Oxyria digyna*. Elsewhere *L. cupreus* has also been reported to utilize *O. digyna*, while *L. phlaeas* often uses *Rumex* (Ferris, 1974). The ground color of both species is green in California, but *L. phlaeas* larvae from Asia and Europe may be

pink or green and some California (and Old World) specimens have a pinkish dorsal and/or lateral line (fig. 74-3b). In California they are distinguishable from other *Lycaena* species by their darkly pigmented head and legs, pale prothoracic shield (figs. 33, 34), and lack of prominent dorsal setae. All dorsal and lateral setae on T2-A8, aside from mushroom setae, are uniformly short, erect, tapered, and brownish. In California *L. cupreus* larvae these setae are shorter than the sensory setae and about as long as the spiracle width, while in *L. phlaeas* at least some are longer than the sensory setae and about twice as long as the spiracle width. Larvae of *L. cupreus snowi* (Edwards) from Colorado have setae about as long as those of *L. phlaeas*. Larvae of *L. phlaeas* examined from Corsica, Japan, and the eastern U.S. are similar to California specimens in setation but have much lighter crania and legs.

Another group with similar biologies and larval morphology consists of *L. editha, L. rubidus*, and *L. xanthoides*. Larvae of all three feed on *Rumex* and are myrmecophilous; old records of *L. editha* larvae feeding on *Horkelia* and *Potentilla* (Rosaceae) (reiterated by Johnson and Balogh, 1977 and Pyle, 1981) are not supported by our observations. The ground color of these larvae varies from green to maroon or rust-red and often there is a maroon middorsal line (fig. 74-3c). All dorsal and lateral setae are erect to suberect and, except for mushroom setae, brownish. The most distinctive features of these larvae are well developed dendritic setae near the spiracles, especially on T1, A7, and A8 and short clavate-capitate setae dorsal to the spiracles, especially on A7 and A8 (fig. 15). In each species the cranium and prothoracic shield are dark; *L. editha* and *L. rubidus* also have dark legs. The head and prothoracic shield of *L. xanthoides* are lighter than in the other species (figs. 42-44); dendritic setae usually occur only near the spiracles on T1, A7, and A8, but in some populations these setae also occur on A1-A4. In *L. editha* and *L. rubidus* larvae dendritic setae are present near the spiracles on T1, A7, A8, at least some of segments A1-A6, and frequently laterally on T2 and T3. The larvae of *L. editha* and *L. rubidus* differ in prothoracic shield setation as described in the key. *Lycaena editha* and *L. rubidus* are sometimes sympatric and occur mostly above 2000m in central and northern California but *L. xanthoides* is more widely distributed, mostly below 2000m, and does not occur with the others. Adults of *L. editha* found below 2000m in the vicinity of Mount Shasta are similar (especially in size) to *L. xanthoides* and have been considered inter-mediate between those species (Scott, 1980); but larvae from this population (at Dunsmuir and Mount Shasta City) are more similar to Sierra Nevadan *L. editha* and key to that species.

Two other closely allied species are *L. gorgon and L. heteronea*. They are distinguished from the other *Lycaena* species by the use of *Eriogonum* as a larval host and by the presence of numerous nonpigmented, recumbent setae at least twice as long as the spiracles. These setae have a finely granular surface giving them a whitish appearance. The larval

color is pale turquoise to green for *L. gorgon* (fig. 74-2a) and dull blue-green to green for *L. heteronea* (fig. 74-2c); both species are faintly mottled but devoid of strongly contrasting markings; some *L. heteronea* larvae have a pale yellow or white lateral line. The cranium is nonpigmented in *L. gorgon* (fig. 37) and nonpigmented to somewhat brownish in *L. heteronea* (fig. 38). *Lycaena heteronea* occurs mostly above 1500m from Mount Pinos in Ventura Country northward through the Sierra Nevada, Cascade, and Warner ranges and at sea level along the coast near Point Reyes. *Lycaena gorgon* is primarily cismontane in distribution below 1500m but also occurs up to about 2000m along the east slope of the Sierra Nevada from southern Mono County southward and in the Warner Mountains.

Usually these species are easily distinguished according to their setation. *Lycaena heteronea* has distinct dorsal prominent setae (usually somewhat melanic) on T2-A8 and erect dendritic setae near the spiracles on A7 and A8 (also occasionally on T1 and rarely on the prothoracic shield); nonprominent dorsal setae are mostly 1.5-2X as long as the spiracle width. *Lycaena gorgon* lacks both prominent dorsal setae and dendritic setae; the dorsal setae are mostly 2-4X as long as the spiracle width. But in *Lycaena gorgon* larvae from the Warner Mountains of Modoc County the setae are more erect (recumbent to suberect) than in larvae from elsewhere and some dorsal setae may be nearly as erect as the dorsal prominent setae of *L. heteronea*. Occasionally, they also have 1-2 erect (but not dendritic) setae near the A7 and A8 spiracles. Larvae of *L. heteronea* from near Mount Lassen resemble those of *L. gorgon* from the Warner Mountains in setal erectness; their dorsal prominent setae are less erect and less distinct than in other populations of *L. heteronea* and are nonpigmented. In these larvae the dendritic setae near the spiracles on A7 and A8 are poorly developed; there may be only 3-4 of them and with lateral spicules very short and confined to the apex. In both of these populations the mandibles frequently have three setae but other populations of both species typically have two mandibular setae.

Lycaena hermes larvae differ greatly from those of the other *Lycaena* species in host, range, and morphology. They feed on *Rhamnus crocea* (Rhamnaceae) and are restricted to San Diego County and northern Baja California, Mexico. They are bright, light green without strongly contrasting markings (fig. 74-2b), though a pair of pale yellowish dorsal lines may be present. These larvae may appear glabrous since all dorsal and lateral setae on T2-A8 are sparsely scattered, subequal in length to the spiracles, and recumbent; the setae are lightly pigmented and weakly tapered to blunt-tipped. The sensory setae on the prothoracic shield are at least twice as long as all other dorsal and lateral setae on T2-A8 and subequal to the longest setae at the anterior margin of the prothorax; they may be filiform or tapered, as in other *Lycaena* species, or apically truncate-spatulate (fig. 21). The cranium is nonpigmented and the prothoracic shield is rather small and narrow (fig. 39).

The larvae of the four remaining *Lycaena* species are similar in setation but different in biology. *Lycaena helloides* and *L. nivalis* feed on *Polygonum* and (at least in the lab) *Rumex* (Polygonaceae); some populations of *L. helloides* also feed on *Potentilla* (Rosaceae) (Shapiro, 1974). *Lycaena arota* feeds on *Ribes* (Saxifragaceae) and *L. mariposa* feeds on *Vaccinium* (Ericaceae) (Pratt and Ballmer, 1986). They have well-defined dorsal prominent setae on T2-A8 while most other dorsal and lateral setae (not mushroom setae) on T2-A8 are erect to recumbent and more-or-less tapered but apically truncate (figs. 2c, 2d). In *L. arota* dorsal setae on T2 posterolateral to the shield are curved caudad (fig. 23) while in the other species these setae are curved cephalad (fig. 24). The ground color is green for all four species. Some populations of *L. arota* (especially in southern California) have white or yellowish paired dorsal and lateral lines (fig. 74-1d). Larvae of *L. nivalis* sometimes have a maroon middorsal line and an indistinct yellowish lateral line (fig. 74-3a); some larvae of *L. helloides* and *L. mariposa* also have an indistinct yellowish lateral line (fig. 74-2d). Cephalic infuscation in *L. nivalis* extends across the front of the head and posteriorly well beyond the ocelli (fig. 36), while in *L. arota* (fig. 35) and *L. helloides* (fig. 40) it is limited to a narrow cresent connecting ocelli 1-5. In *L. mariposa* (fig. 41) cephalic infuscation varies from nearly as extensive as in *L. nivalis* to virtually absent. Although *L. helloides* is multivoltine (diapause stage not known) and widely distributed (mostly below 2000m) the others are univoltine and mostly confined to higher elevations in central and northern California.

Theclinae

The most distinctive features of the California thecline larvae are the head width (ca half as great as the body), lack of eversible tubercles, and presence of buttressed chalazae. The prothoracic shield is sclerotized, frequently brownish, and lacks secondary setae longer than the sensory setae; the head color ranges from yellowish to dark brown. The single representative of the tribe Theclini, *H. grunus*, lacks a honey gland, has a broadly diamond-shaped prothoracic shield (broadly rounded posterior to the sensory setae), five mandibular setae, and a biordinal lateroseries of crochets. All other species belong to the tribe Eumaeini. They have a honey gland, a more-or-less 't'-shaped prothoracic shield (abruptly constricted posterior to the sensory setae), usually two mandibular setae, and lack crochet lateroseries on the prolegs. In general appearance, thecline larvae (especially *H. grunus*) are most similar to those of the Lycaeninae; they may be distinguished from the latter by the presence of buttressed chalazae, setae on the prothoracic shield lateral to the sensory setae, usual presence of a honey gland, and absence of mushroom setae.

Among the Eumaeini two groups may be distinguished according to setation. In one group consisting of *Atlides, Callophrys, Ministrymon*, and *Strymon* all setae are cylindric, tapered, and straight or slightly

curved with dendritic setae absent or inconspicuous (often poorly developed or obscure) and confined to the margins of the honey gland. Also in this group, the sensory setae are filiform to slightly clavate (branched in *Atlides*) and often have conspicuous lateral spicules; the mandibles have two setae. The other group, consisting of *Harkenclenus* and *Satyrium*, has a broad range of setal forms including erect, recurved, tapered, and clavate; dendritic setae occur prominently around the honey gland and often on other segments, while other dorsal setae on A7 and A8 are often recumbent or somewhat capitate. Also in this group, the sensory setae are filiform, tapered, or spatulate and have inconspicuous lateral spicules; the mandibles have 2-6 setae. Coincidentally, diapause occurs as pupae in the former group and as ova in the latter. Most California thecline species are univoltine and restricted to a few closely related larval hosts. A few species are bi- or trivoltine, while only *S. melinus* is continuously brooded and known to utilize a wide range of larval hosts.

Atlides

The single California species, *A. halesus*, occurs throughout the state but is more abundant in the south. It is often encountered in lowland riparian habitats where the larval mistletoe host may be abundant. Features which distinguish larvae of this species from other California theclines include a velvety texture due to an even distribution of short reddish-brown setae (no prominent setae), uniform green color (fig. 74-4a) (rarely obscurely mottled), presence of mushroom chalazae (fig. 26), branched sensory setae (fig. 6), a white prothoracic shield outlined in black (fig. 45), and use of *Phoradendron* (Viscaceae) as a larval host. There are 3-4 annual broods in the south, but probably 2-3 in the north; the pupae overwinter.

Callophrys

The genus *Callophrys* was redefined by Clench (1961) to contain six subgenera three of which (*Callophrys, Incisalia*, and *Mitoura*) occur in california; some authors including Miller and Brown (1981) give these taxa full generic status. The systematics of this group is in need of review and it seems unlikely that any study lacking comprehensive biological, morphological, and/or biochemical data can resolve existing controversies. The morphology of mature larvae is useful in distinguishing some subgenera, but of little use in distinguishing most species. Yet the taxonomic limits of both species and subgenera are often definable by biological differences such as host preference, habitat selection, and number of instars.

In California, we provisionally recognize four species each in the subgenera *Callophrys* and *Incisalia* and six in *Mitoura*; Scott (1986) recognizes only three species each of *Callophrys* and *Mitoura* in

California, but his evidence is not compelling. Adding to the confusion is a recent nomenclatural change; the name *C. dumetorum*, previously applied to most lowland *Callophrys* populations in California, properly refers only to those along the central coast previously known as *C. viridis* (W. H. Edwards), which is now relegated to a junior synonym (J. F. Emmel, *in litt.*). The name *Callophrys perplexa*, formerly considered the southern California subspecies of *C. dumetorum* (in its former usage), now becomes the senior synonym and must be applied to the remaining lowland cismontane populations of this species.

There is little difference in larval morphology among the California species of *Callophrys* and *Incisalia* (and also *Strymon*). All are covered with erect, straight, tapered setae of varying lengths which are non-pigmented or pale brown and apically darkened. Prominent setae on T2-A6 are absent or obscure. The sensory setae are filiform to slightly broader in the apical half and have conspicuous lateral spicules (fig. 7); rarely one or both may be bifurcate. Dorsal prominences on T2-A6 are weakly to moderately developed, while those on T1 anterior and posterior to the prothoracic shield are weakly developed. The most prominent dorsal setae on T1 posterolateral to the shield are arranged in one or two transverse rows (fig. 7). Relatively inconspicuous dendritic setae occur near the honey gland. The head is yellowish-brown with darker pigment confined to an arc connecting ocelli 1-5 but not extending to ocellus 6 (fig. 59) or the entire anteroventral half of the head may be dark brown, broadly enclosing all ocelli (fig. 60).

Mitoura larvae are easily distinguishable from those of the other subgenera. Those species which utilize Cupressaceae as a larval host have well developed dorsal prominences on T1 anterior and (especially) posterior to the prothoracic shield often causing it to appear sunken; the most prominent setae on the prominences posterior to the shield are randomly distributed (fig. 8); dendritic setae are absent. In those species which utilize Viscaceae as a larval host the dorsal prominences on T1 posterior to the shield are poorly developed and have prominent setae arranged in a transverse row (as in the other subgenera) or absent (fig. 73); but distinct dorsal prominences are present at least on T2 and A6; they also have dendritic setae near the honey gland.

No consistent morphological distinctions were found to separate larvae of *Callophrys* and *Incisalia*. Larvae of species in these subgenera are best distinguished according to distribution and host plant. In California *Callophrys* larvae utilize *Eriogonum* (Polygonaceae) and *Lotus* (Fabaceae), while *Incisalia* larvae feed on various hosts in other plant families. There are four larval instars in all species of these subgenera in California.

Cephalic pigmentation is useful in distinguishing some *Callophrys* populations. Larvae of *C. dumetorum* (formerly *C. viridis*) from near San Francisco and *C. perplexa* (formerly *C. dumetorum*) from southern California have dark cephalic pigment narrowly confined to ocelli 1-5

(fig. 59). In larvae of most other California *Callophrys* populations the head is dorsally yellowish-brown and ventrally dark brown with dark pigment broadly enclosing all ocelli (fig. 60), but larvae of *C. dumetorum* from near Monterey are variable in cephalic pigmentation. The dorsal profile can also be used to discriminate some taxa. The dorsal prominences in *C. comstocki, C. dumetorum*, and *C. lemberti* often (but not invariably) create a saw-toothed profile (fig. 74-4b), while those in *C. perplexa* are more rounded (fig. 74-4c). All the *Callophrys* species use *Eriogonum* as a larval host; *C. perplexa* also commonly uses *Lotus crassifolius* and *L. scoparius; C. dumetorum* is reported to use *L. scoparius* in the San Francisco area (Gorelick, 1971). *Callophrys comstocki* occurs in several Mojave Desert mountain ranges; *C. perplexa* occurs throughout cismontane California up to ca 1500m; *C. lemberti* occurs generally above 2000m in the Cascade, Sierra Nevada, Siskiyou, and Warner Mountains; *C. dumetorum* is strictly coastal and associated with *Eriogonum latifolium* from northern Monterey County to Sonoma County (G. Gorelick, personal communication). Although *C. comstocki* is at least partially bivoltine, the other species are univoltine. Larval ground color is usually green, pale pink, or yellow; dorsal and lateral lines and dorsolateral chevrons may be present or absent.

Morphological differences among *Incisalia* larvae are too small to aid greatly in identification. The larval morphology of *I. eryphon* is most divergent, as indicated in the species key. But the larvae of all the species are best identified according to host and locality. As with some members of *Callophrys*, the *Incisalia* larval head is yellowish-brown with dark pigment confined to a narrow arc linking ocelli 1-5. Larvae of *I. augustus*, the most widespread species, can be found in most areas except the deserts on several hosts, especially *Adenostoma, Heteromeles, Prunus* (all Rosaceae), *Ceanothus, Rhamnus* (both Rhamnaceae), and *Cuscuta* (Convolvulaceae); Powell (1968) also confirms that it uses *Arbutus menziesii* Pursh. (Ericaceae) and *Chlorogalum pomeridianum* (D. C.) Kunth. (Liliaceae). Larvae of *I. eryphon* occur on *Pinus* (Pinaceae) usually above 2000m from the San Bernardino Mountains northward through the Cascade, Sierra Nevada and Siskiyou Mountains. Larvae of *I. fotis* feed on *Cowania mexicana* var. *stansburiana* (Rosaceae) in mountains of the Mojave Desert. Larvae of *I. mossii* feed only on Crassulaceae; primarily they utilize *Sedum* but some populations also use *Dudleya* (J. F. Emmel, personal communication); this species occurs in isolated cismontane colonies from the San Bernardino Mountains northward. *Incisalia augustus* is partially bivoltine, especially in the south, but the other species of *Incisalia* are univoltine.

Coloration can be useful in identifying live larvae of some *Incisalia* species. Larvae of *I. augustus* (fig. 74-4d) and *I. fotis* are polymorphic and often resemble members of the nominate subgenus. Their ground color is usually green and they frequently have white or red and white dorsolateral chevrons and lateral lines; and they often have at least a

trace of a reddish lateral bar on A1 (fig. 74-4d). Larvae of *I. mossii* are red or greenish-yellow and may have whitish lateral chevrons. Larvae of *I. eryphon* are monomorphic with a green ground color and paired yellowish white dorsal and lateral lines (fig. 74-5a).

The *Mitoura* species can be divided into two groups based on biology and larval morphology (as described above). Those which feed on cedar, cypress, and juniper (Cupressaceae) have 5−7 larval instars, whereas those which feed on dwarf pine mistletoe (Viscaceae) have five larval instars. The Cupressaceae-feeders have well developed dorsal prominences on T1 anterior and (especially) posterior to the prothoracic shield but segments T2-A6 are dorsally rounded, lacking prominences. These larvae are dark green with white dorsal and lateral lines which are weakened or broken intersegmentally, as illustrated for *C. (M.) nelsoni* (fig. 74-5b); they are densely covered with erect straight setae ca twice as long as the spiracle diameter; dendritic setae are absent. The Viscaceae-feeders are more angulate with paired dorsal prominences at least on T2 and A6 and weak lateral prominences along the lateral fold (best developed on A7 and A8); but dorsal prominences on T1 are poorly developed or absent (fig. 73). All dorsal setae (except those surmounding dorsal prominences) are shorter than the sensory setae and at most subequal in length to the spiracle width. Prominent setae subequal in length to the sensory setae are present on T1 posterolateral to the prothoracic shield in *C. (M.) johnsoni* but not in *C. (M.) spinetorum*. The ground color of these larvae is yellow to olive-brown, while the dorsal prominences are usually brighter yellow, bordered laterally by white and dark brown, and often reddish apically (fig. 74-5c). A transverse bar may be apparent as a darkening of the dorsal prominences on A1. These larvae appear to glisten due to a shinier body surface and shorter, sparser setae than in the Cupressaceae-feeders; their setae are often reclinate toward the apices of the dorsal prominences (fig. 4); a few inconspicuous dendritic setae occur at the margin of the honey gland.

The California *Mitoura* species which feed on Cupressaceae comprise a portion of a complex of several often narrowly allopatric sibling species and/or subspecies occurring throughout most of North America. These may be poorly distinguishable where their ranges converge and are perhaps best considered ecotypic components of a superspecies. Yet in spite of a few areas of possible intergradation (Shields, 1985; Scott, 1986), the California taxa are relatively uniform throughout their ranges which may be parallel and narrowly separate (by altitude and habitat) over long distances. Thus, *M. nelsoni* occurs in association with *Libocedrus decurrens* in montane habitats from San Diego County to Oregon, while *M. loki* and *M. siva* often occur at different elevations and in association with other hosts in the same mountains. The larvae of these species are best distinguished according to host and locality.

Although larvae of most (probably all) of the Cupressaceae feeders can be reared on many plants in that family, most populations are

associated with one host species in nature (Johnson, 1978). Four subspecies of *M. siva* occur in California; *M. s. siva* is associated with *Juniperus osteosperma* in the mountains of the eastern Mojave Desert; *C. (M.) s. juniperaria* (J. A. Comstock) is associated with *J. californica* from the lower northwest slopes of the San Bernardino Mountains westward along the northern edge of the San Gabriel Mountains (where it is also associated with *J. osteosperma*) to the eastern edge of the Tehachapi Mountains; *C. (M.) s. mansfieldi* (Tilden) is associated with *J. californica* in the inner coast ranges from Ventura County to San Benito County; *C. (M.) s. chalcosiva* Clench is associated with *J. occidentalis* in the Inyo and White Mountains. The status of brown *M. siva* (or *M. nelsoni*) populations associated with *J. occidentalis* in the San Bernardino Mountains, Sierra Nevada, and Modoc County is uncertain; these may be conspecific with *C. (M.) barryi* Johnson described from eastern Oregon. There are two subspecies of *Mitoura nelsoni*; the nominate one ranges from the mountains of San Diego County northward in association with *Libocedrus decurrens; C. (M.) n. muiri* (Hy. Edwards) is associated with *Cupressus sargentii* and (rarely) *J. californica* (J. Lane, personal communication) in coastal mountains from San Luis Obispo County to Mendocino County. *Mitoura loki* occurs with *J. californica* from the eastern San Bernardino Mountains southward to Baja Californica. *Mitoura thornei* is known only from Otay Mountain in San Diego County in association with *Cupressus forbesii. Mitoura nelsoni* is univoltine, but at least some populations of the other species are partially bi- or trivoltine.

Habrodais

One species of *Habrodais, H. grunus*, occurs in montane habitats throughout California except in the deserts. The larval hosts are *Quercus chrysolepis* and, according to Pyle (1981), *Q. vaccinifolia* Kell., *Chrysolepis chrysophylla* (Dougl.) A. DC., and *Lithocarpus densiflora* (H. & A.) Rehd., all in the Fagaceae. *Habrodais grunus* is the only California member of the tribe Theclini and differs considerably from the other theclines. The most obvious differences are the lack of a honey gland, presence of a lateroseries of crochets (fig. 72a), and an evenly convex posterior margin of the prothoracic shield (fig. 46). It also lacks dendritic setae and the sensory setae are finely tapered with minute lateral spicules confined to the apex. The ground color is pale blue-green (including the prothoracic shield) and a pair of pale yellow subdorsal lines may be present (fig. 74-3d). A pair of prominent dorsal setae occurs on segments T2-A8, while other dorsal setae are bent parallel to and flattened in the body plane. This species is univoltine with egg diapause.

Harkenclenus

The single member of this genus, *H. titus*, ranges from coast to coast but in California it is confined to the northeastern corner southward in the

eastern Sierra Nevada to near Lake Tahoe. Larvae feed on *Prunus virginiana* and are distinctively marked reddish dorsally on T2, T3, and A6 and dorsally and laterally on A7-A10; the remainder of the body is green (fig. 74-5d). The head is dark brown in a band across the frons and posteriorly to the ocelli, but lighter dorsally (fig. 47). Aside from some members of *Satyrium*, this is the only California thecline with dendritic setae present beyond the margin of the honey gland on A7. Dendritic setae occur laterally near the spiracles or in that latitude on T1-A1, A7, and A8, with the greatest numbers (ca 20) on T3 and A1. All setae are orange-brown, erect, and straight. Prominent setae on T2-A6 are indistinct, but the longest setae (dorsally and along the lateral fold) are ca 2.5X as long as the spiracle diameter. This species is univoltine with egg diapause.

Ministrymon

One member of this genus, *M. leda*, inhabits the southern California deserts. It is multivoltine and larvae feed primarily on *Prosopis* but we have one record on *Acacia greggii* (both Fabaceae). They are distinctively marked green and white (fig. 74-6a) and segments T2-A6 have dorsal prominences which confer a saw-toothed dorsal profile (fig. 56c). Each dorsal prominence is surmounted by 1-4 prominent setae ca 3-4X as long as the spiracle diameter; most other dorsal setae are 1-2X as long as the spiracle diameter.

Satyrium

Seven members of this genus occur in California; all are univoltine with egg diapause. Although morphologically more diverse than other California thecline genera, the *Satyrium* species are united by the presence of at least 20 dendritic setae on A7, especially along the margin of the honey gland; four species also have dendritic setae on other segments. Among other California theclines only *H. titus* shares such an abundance of dendritic setae. Distinct dorsal prominences may be present, but more often there are weakly developed dorsal ridges extending from T2-A6, so that in cross-section the body appears trapezoidal with the dorsal area flat or somewhat concave and the lateral areas sloping outward to the lateral folds. Prominent setae of variable number and degree of distinctness occur along the dorsal ridges and the lateral fold. Other setae may be recumbent to erect and nonpigmented to dark brown. Cephalic pigmentation varies from yellow to dark brown.

Satyrium auretorum occurs throughout cismontane California in chaparral and scrub oak woodland. Larvae feed on various oaks, especially the scrub oaks, *Quercus cornelius-mulleri, Q. dumosa*, and *Q. wislizenii*. They are green with a yellow lateral line of variable intensity and often ventrally bordered with pink (best developed on T2, T3, A7 and A8) (fig. 74-6b). The head is dark brown anteroventrally (across the frons and extending posterolaterally beyond the ocelli), but yellowish

brown apically (fig. 51). The sensory setae are tapered, ca 5X as long as other setae on the shield, and 1.5X as long as the longest dorsal setae posterolaterally adjacent to the shield. Prominent dorsal and lateral setae, ca 2X as long as the spiracle width, occur in groups of 2-10 on T2-A6 (fig. 56b). Nonprominent dorsal and lateral setae on T2-A6 are weakly spindle-shaped, suberect, straight to moderately bent, and ca 1-1.5X as long as the spiracles; on A7 they are shorter and more strongly bent (often parallel to the body). These setae are reddish brown, minutely dentate, and tapered. Dendritic setae are confined to A7.

Satyrium behrii ranges from the Little San Bernardino Mountains west to the Mount Pinos area, northward along the east slope of the Sierra Nevada to Oregon, and in the Panamint and White Mountains. The larvae feed on *Purshia glandulosa* and *P. tridentata*. The ground color is dark green with white or yellow middorsal and lateral lines and dorsolateral chevrons on T2-A6 (fig. 74-6c). The head is mostly yellowish brown, but dark pigment extends across the frons and posterolaterally beyond the ocelli (fig. 52). A pair of prominent dorsal setae ca 3-4X as long as the spiracle width occurs on T2; lateral prominent setae are present on A7 and A8 but usually absent elsewhere. Most other dorsal and lateral setae are 1-2X as long as the spiracle width, bent parallel to and flattened in the plane of the body surface, and acutely tapered. Dendritic setae occur in groups of 4-6 subdorsally on T2 and T3 as well as around the honey gland.

Satyrium californica occurs throughout the state except in the eastern deserts. Larvae have been found on *Ceanothus* and *Quercus*, but additional hosts are likely since the butterfly sometimes occurs in the absence of those plant genera. The ground color is chocolate brown dorsally and white ventrally (fig. 74-6d); the head (fig. 53), legs, chalazae, and most setae are dark brown. Conspicuous dendritic setae ca 1-3X as long as the spiracle width are present on T1-A7. While dorsal and lateral prominent setae on T2-A6 are ca 5-7X as long as the spiracle width, other dorsal and lateral setae on those segments are sparse and 1/4-1X as long as the spiracle width. Since larvae are usually found in early morning they may be nocturnal, as with *S. edwardsii* (Grote and Robinson) in the eastern United States (Webster & Nielson, 1984).

The larva of *S. fuliginosum* superficially resembles that of the polyommatine *I. icarioides* in habits and appearance more than the larvae of its congeners. The ground color is light green with whitish lateral chevrons (fig. 74-7a), the head is dark brown (fig. 48), and the body dorsum is evenly convex. Dorsal prominent setae (ca 2-5X as long as the spiracles) are present on T2 but absent or obscure posteriorly; lateral prominent setae are more abundant and conspicuous on T1-T3 and A6-A10 but may be absent on the intervening segments. Dendritic setae ca 2X as long as the spiracles are present posterolateral to the prothoracic shield, near the spiracles (or in the same latitude) on T3-A6, and around the honey gland. The remaining dorsal and lateral setae are

numerous, ca .5-IX as long as the spiracles, erect, tapered, and light brown. The larvae feed on *Lupinus* and are strongly myrmecophilous; they probably feed nocturnally, but during the day they can be found at the base of host plants and under nearby rocks. This species occurs along the eastern slopes of the Sierra Nevada northward through the Cascade, Siskiyou, and Warner Mountains.

The larva of *S. saepium* differs from its congeners (except *S. auretorum* and *S. sylvinus*) in having dendritic setae confined to the lateral margins of the honey gland. These setae are ca as long as the spiracles, clavate, and have very short lateral spicules. The following combination of characters distinguish this species from all others: the sensory setae are slightly spatulate in the apical fourth, ca 4-5X as long as the spiracles and nearly all other dorsal and dorsolateral setae on T2-A6; prominent dorsal setae are absent; the dorsal and lateral setae are of two forms intermixed, one of which is brownish, suberect, and cylindric and the other is nonpigmented, coarsely dentate, spindle-shaped, basally bent nearly parallel to the body surface, and compressed in that plane (as in fig. 18). Dendritic setae occur only on A7. The ground color is dull, dark green; a yellow lateral line extends from T2 to A10 and is most prominent on A8. Cephalic infuscation is limited to a diffuse band across the ocellar region (fig. 49). Larvae feed on *Ceanothus* and occur throughout the state except in the eastern deserts.

Satyrium sylvinus is also widespread in California, but absent from the Colorado and Mojave Deserts. Larvae feed on *Salix* (Salicaceae). They are light green with distinct white subdorsal and lateral lines and somewhat less distinct lateral chevrons (fig. 74-7b). The head is yellowish with dark pigment confined to a narrow band connecting ocelli 1-5 (fig. 50). The sensory setae are finely tapered, ca 3-5X as long as the spiracles and other setae on th shield, and subequal to the longest dorsal prominent setae posterolateral to the shield and on T2. Dorsal prominent setae on T3-A6 are ca 2X as long as the spiracles and other dorsal and lateral setae on those segments. All setae are tapered, suberect, and nonpigmented. Nonprominent dorsal and lateral setae on T2-A6 are erect to strongly bent; those on A7 are often bent parallel to the body. Dendritic setae are confined to A7. The body is somewhat angulate in cross-section due to a rather flat or slightly concave dorsum (less noticeable in distended specimens).

Satyrium tetra has about the same distribution as *S. saepium*, being found in chaparral habitats containing its host, *Cercocarpus* (Rosaceae). Larvae resemble those of *S. sylvinus* in coloration, but have less well developed dorsal and lateral lines and more prominent lateral chevrons (fig. 74-7c). A slightly broader band of dark pigment surrounds the ocelli (fig. 54). They are also distinctive in being covered with erect and relatively short orange-brown setae. The sensory setae are slightly spatulate, as in *S. saepium*, and subequal to the longest dorsal setae posterolaterally adjacent to the shield and on T2. Dorsal prominent

setae occur in groups of ca 20 on T2-A6 and are ca 2X as long as other dorsal and lateral setae on those segments (fig. 56a). Clavate dendritic setae occur on the prothoracic shield near the sensory setae and on A7. All other dorsal and lateral setae are tapered. The body is rather flat dorsally between the rows of dorsal prominent setae resulting in an angulate cross-section even more pronounced than in *S. sylvinus*.

Strymon

Larvae of the three *Strymon* species in California are very similar to each other and to larvae of *C. (Callophrys)* and *C. (Incisalia)*. They are covered with nonpigmented (except apically darkened), erect, straight, tapered setae; prominent setae on T2-A6 are absent or obscure (not much longer than surrounding setae) and dendritic setae are inconspicuous and confined to the margin of the honey gland. They differ from larvae of *Callophrys (Callophrys)* and *C. (Incisalia)* by their more filiform and less prominently spiculate sensory setae, smaller head, and by slight differences in cephalic pigmentation. Dark infuscation on the head is confined to an arc connecting ocelli 1-5 and extending posteriorly to ocellus 6 (figs. 65-67), whereas in *C. (Callophrys)* and *C. (Incisalia)* the cephalic infuscation is usually either more extensive (broadly encompassing all ocelli) or limited to ocelli 1-5. The ratio of the head width to the distance between insertions of the sensory setae on the prothoracic shield is usually at least 2.2 in both *S. avalona* and *S. melinus*, about 2.0 in *S. columella*, and usually less than 2.0 in *C. (Callophrys)* and *C. (Incisalia)*.

Strymon melinus occurs throughout the state and probably has the widest host range of any North American lycaenid. In California its larvae are most often found on *Eriogonum* (Polygonaceae) and various members of the Fabaceae and Malvaceae. *Strymon avalona* occurs only on Santa Catalina Island and utilizes *Eriogonum* (Polygonaceae) and *Lotus* (Fabaceae) (Gorelick, 1987). *Strymon columella*, largely subtropical in distribution, occurs in southern California and utilizes *Hibiscus, Sphaeralcea*, and other Malvaceae as larval hosts. The larvae of *S. columella* can be distinguished from those of *S. melinus* by the milky color of their chalazae; this character is best seen in live larvae. Other differences include a narrower host range and smaller distribution. The limited distribution of *S. avalona* may be the best clue to distinguish it from *S. melinus*; also, its head is slightly browner and the ocellar infuscation is a little darker and more extensive (fig. 65), but otherwise they are virtually indistinguishable.

Polyommatinae

All California members of this subfamily belong to the tribe Polyommatini. The head is about 1/4 as broad as the body and almost always black (but lighter brown in two local species and nonpigmented in many

exotic species); most species have a honey gland and eversible tubercles; the prothoracic shield is nonsclerotized, nonpigmented (although there may be dark chalazae), and often has a smoothly convex anterior margin; the bases of the sensory setae may appear sunken below the cuticular surface due to the height and density of cuticular ridges. The chalazae frequently appear stellate due to distolateral points. Prominent setae (at least subequal to the length of sensory setae) commonly occur on the prothoracic shield. The majority of species in this subfamily are univoltine and active in spring or summer, but some species and/or subspecies appear in late summer or fall; a few species are facultatively bi- or trivoltine while others are multivoltine.

Agriades

One species of this genus, *A. franklinii*, occurs in California usually above 3000m in the Cascade and Sierra Nevada Mts. but as low as 2000m in the Siskiyou Mts.; it is associated with wet meadows and boggy stream and lake margins. This species is partially bivoltine with diapause in the second instar. Eggs and larvae were found on *Dodecatheon alpinum* (Gray) Greene (Primulaceae) near Sonora Pass. The larvae mine the leaves until the last instar. This is the only polyommatine in California which lacks both a honey gland and eversible tubercles. Other distinguishing features include the dark brown color of setae (even ventrally), spiracles, and legs. Distinct dorsal and lateral prominent setae are present, and all setae are erect and straight to slightly curved; chalazae are distinctly stellate. The ground color is deep, bright green and there is a red middorsal line (fig. 74-7d).

Brephidium

One member of the genus *Brephidium, B. exilis*, is widespread in California. It is multivoltine and occurs commonly in relatively xeric and saline habitats where its major hosts, *Atriplex, Chenopodium*, and *Salsola* (Chenopodiaceae) thrive; *Sesuvium verrucosum* (Aizoaceae) is also used in some areas (Johnson, 1981). Larvae are various shades of green and usually without distinct markings (fig. 74-8a); often the body appears finely granular or pollinose. Prominent setae (2-3X as long as the spiracles) occur only along the anterior margin of T1, laterally on T2, and along the posterior margin of A9-10. All other dorsal and lateral setae are clavate-capitate, often bent parallel to the body surface, and ca as long as the spiracle width. All setae are nonpigmented and chalazae are weakly stellate. The sensory setae are finely tapered and at least twice as long as all other dorsal setae on T2-A8. Dendritic setae are absent.

Celastrina

One species, *C. argiolus*, occurs throughout California in many habitats but not in the desert lowlands. In California the larvae utilize

primarily *Ceanothus* (Rhamnaceae) and many hosts in the Rosaceae; they are rarely found on *Lotus* (Fabaceae) (Gorelick, 1987). In Arizona they also utilize *Amorpha (Fabaceae)* (Noel McFarland, personal communication) and *Eriogonum* (Polygonaceae). Larvae prefer to feed on flowers, buds, and immature fruit. Adults fly in spring and early summer throughout most of California and are partially bivoltine (at least in southern California) with pupal diapause. Most setae are bent parallel to the body surface and arise from strongly stellate chalazae (fig. 2f). The chalazae are crowded and their lateral points are often so long (the span between opposite points may be nearly as great as the setal length) that they may interdigitate; only *L. marina*, among other California species, approaches this condition. The sensory setae on the prothoracic shield are slightly expanded and flattened in the apical third (ca 2X as broad as the basal width) and are ca 3-4X as long as other setae on the shield; their length is subequal to a pair of prominent dorsal setae on T2 and ca 2-3X as long as all other dorsal setae on T2-A6. A few dendritic setae occur at the lateral margins of the honey gland and lateral to the sensory setae on the prothoracic shield. Larvae are polymorphic in coloration. The ground color is often whitish, pale pink or pale green; distinct lateral lines and chevrons are lacking but a conspicuously dark green, pink, or brownish transverse bar usually occurs on A1. A color morph common for larvae found on *Adenostoma fasciculatum* is illustrated in fig. 74-8b.

Euphilotes

The genus *Euphilotes* is extremely complex with four species and numerous subspecies in California. One member, *E. mojave*, is often considered a subspecies of *E. enoptes* (Pratt and Ballmer, 1987). All *Euphilotes* larvae feed on buds, blossoms, and seeds of *Eriogonum*. Several hosts may be used by one species, but most local populations use a single host and only rarely do sympatric species (and subspecies) share a host. All members of this genus diapause as pupae and are typically univoltine; some populations of *E. enoptes* are facultatively bi- or trivoltine (Pratt and Ballmer, 1987). Published reports of five larval instars in *E. enoptes bayensis* (Langston) and *E. e. smithi* (Mattoni) by Langston and Comstock (1966) and Arnold (1983), respectively, are probably erroneous since we have found only four instars in hundreds of rearings representing all four *Euphilotes* species. Larval ground color may be white, pink, yellow, or brownish; color pattern ranges from non-patterned to strongly marked with white, pink, yellow, and/or brown middorsal and lateral lines and lateral chevrons (fig. 74-8c). Distinguishing morphological features of this genus include apically spatulate sensory setae (fig. 13), a few dendritic setae at the lateral margins of the honey gland and usually near the A1 spiracles, moderately to weakly stellate chalazae, and a variable number of prominent setae on T2-A6 (sometimes absent).

Larvae of *E. rita* are perhaps the most distinctive of the genus. Paired dorsal prominences on T3-A6 are steeply peaked, creating a saw-toothed lateral profile, and each usually has at least one prominent seta, which may be directed posteromedially (fig. 57c). More prominent setae occur laterally on T2-A10 and dorsolaterally on T2 (and occasionally on other segments). The ground color is white or pink; markings may be absent but usually there are reddish lateral chevrons on T2-A6 and a transverse bar on A1 (fig. 74-8d). The head is dark brown and the legs are a little lighter. Most nonprominent setae are strongly curved and may be bent parallel to the body. The eversible tubercles arise from distinct but low prominences and are everted frequently as the larva crawls; this may be related to the fact that this is the most strongly myrmecophilic member of the genus. This species occurs along the desert slopes forming the southern and western borders of the Mojave Desert, the east slope of the Sierra Nevada and in some of the desert mountains. Host plants include *Eriogonum davidsonii, E. deflexum, E. heermannii, E. kearneyi, E. microthecum, E. plumatella, E. roseum,* and *E. wrightii.* Flight activity ranges from May to September for various populations.

Larvae of *E. mojave* are similar to those of *E. rita* in distribution of prominent setae. But segments T3-A6 are more rounded dorsally (fig. 57b); the eversible tubercles do not arise from dorsolateral prominences; and the legs, although brown, are much lighter than the head. Populations of *E. mojave* occur scattered through the Mojave Desert and desert slopes bordering it. Larvae can be found in spring on the annuals *E. pusillum* and *E. reniforme.*

Larvae of *E. battoides* and *E. enoptes* are best distinguished according to host plant and locality. In both species dorsal prominences are not apparent and dorsal prominent setae are usually absent posterior to T2 (fig. 57a); the legs are nonpigmented; the number of prominent setae in specific locations differs for different populations; and nonprominent setae are generally short and bent parallel to the body surface. *Euphilotes battoides* utilizes *E. fasciculatum* (everywhere), *E. parvifolium* (along the south coast), *E. heermannii* and *E. microthecum* (in the eastern Mojave Desert), and *E. umbellatum* and various cespitose *Eriogonum* species in the Cascade, Sierra Nevada, Siskiyou, and White Mountains. *Euphilotes enoptes* utilizes *E. nudum* everywhere north and west of the San Bernardino Mts., *E. elongatum, E. davidsonii,* and *E. wrightii* everywhere south and east of the San Gabriel Mts., *E. latifolium* and *E. parvifolium* along the central coast, and *E. elatum* and *E. umbellatum* in the Cascade, Sierra Nevada, and Siskiyou Mountains. Various populations of both species fly in spring, summer, or fall.

Everes

Two species of *Everes* occur in California; *E. amyntula* is widespread from sea level to over 3000m throughout the state (except low elevations

of the deserts), while *E. comyntas* occurs in mesic habitats generally below 1000m from the southern San Joaquin Valley northward. One distinctive feature easily separates this genus from all others in California; the spatulate lobes of the prolegs have sharply defined (somewhat scerotized and pigmented) lateral margins, especially basally (fig. 72b). This trait also occurs in *E. argiades* from Japan. The ground color is green, grey, or pinkish grey; a cream lateral line bordered with pink may be present. Both species are at least facultatively multivoltine with diapause in the last instar.

In California these species usually can be distinguished by setation differences, but some populations in the north and along the Sierra Nevada are intermediate. In larvae of *E. amyntula* dendritic setae are few in number and confined to the margin of the honey gland; other dorsal and lateral setae are erect and straight to slightly curved (rarely bent parallel to the body surface). In *E. comyntas* we found a few (ca 4) dendritic setae around the honey gland, and others near the A1 spiracles and occasionally laterally on T3; but Lawrence and Downey (1966) illustrate (in Illinois larvae) ten dendritic setae near the honey gland and report that others may occur near the A2 spiracles. Many dorsal and lateral setae in *E. comyntas* are curved or bent (often parallel to the body surface), especially on A7 and A8. In some (especially southern) populations of *E. amyntula* the eversible tubercles appear to be noneversible, although their location is marked by the usual wrinkled depression encircled by setae. This may be an adaptation to their habit of feeding only inside *Astragalus* seed pods where it is less likely that they would encounter ants. The larvae of *E. comyntas* and northern California populations of *E. amyntula* which commonly feed externally on various herbaceous Fabaceae have fully functional eversible tubercles.

Glaucopsyche

There are two species of *Glaucopsyche* in California; their larvae are often similar to those of *Lycaeides* and some *Icaricia* species. They are densely covered with short, tapered, nonpigmented setae; the sensory setae are finely tapered; chalazae are moderately stellate; and the dorsal setae on A7 and A8 (between the spiracles) are tapered and suberect to strongly recurved. Larvae of *G. piasus* have dendritic setae laterally on T3-A3, A6, and A7; there are 6-8 prominent dorsal setae anteriorly on T2 which are 2-3X as long as the spiracles and slightly longer than the sensory setae; all other dorsal and lateral setae on T1-A6 are erect, tapered, and .5-.75X as long as the spiracles. Larvae of *G. lygdamus* have dendritic setae around the A1 spiracles (also occasionally around the A2 spiracles and laterally on T3) and (less conspicuously) at the lateral margins of the honey gland. They also have 1-3 pairs of dorsal prominent setae on T2-A6 which are .5-1X as long as the sensory setae and 3-5X as long as the spiracles and other dorsal and lateral

setae. In cismontane southern California populations of *G. lygdamus*, nonprominent dorsal and lateral setae on T2-A6 are suberect to strongly curved (often bent parallel to the body); but in populations from northern California and east of the Sierra Nevada from the central Mojave Desert northward these setae are more erect (never bent parallel to the body). Larval coloration is polymorphic for *G. lygdamus*, ranging from concolorous green to pink and yellow with strong chevron markins and a well defined dorsal line (fig. 74-9a). Larvae of *G. piasus* are less polymorphic with a dull green or gray ground color and lateral chevrons (fig. 74-9b). Larvae of *G. piasus* feed only on lupine, while larvae of *G. lygdamus* utilize *Astragalus, Lotus, Lupinus* and *Vicia*. Both species are univoltine, have pupal diapause, and fly in spring or early summer.

Hemiargus

The two California species of *Hemiargus* are multivoltine and generally restricted to the southern and eastern regions. Their larvae greatly resemble those of the *Icaricia acmon* species group with which they share the following characters: finely tapered sensory setae, at least four prominent dorsal setae on T2 and at least two each on T3-A6, few dendritic setae at the lateral margins of the honey gland and occasionally near the A1 spiracles, and the majority of dorsal and lateral setae suberect to bent parallel to the body surface. However, the most strongly bent setae (near the abdominal spiracles and dorsally on A7 and A8) are somewhat spindle-shaped, flattened, and acutely pointed (fig. 21), whereas in the *I. acmon* species group, setae in the same areas are cylindric and apically blunt or truncate (fig. 2m).

Slight differences in setation distinguish these species. Larvae of *H. ceraunus* sometimes have a few dendritic setae near the A1 spiracles; also, the longest dorsal setae on T2 are no more than .75X as long as the longest setae on the prothoracic shield; and segments T3-A6 have one (or no) pair of dorsal prominent setae (fig. 58a). Larvae of *H. isola* lack dendritic setae near the A1 spiracles; the longest dorsal setae on T2 are at least as long as the longest setae on the prothoracic shield; and there are usually at least two pairs of prominent setae on T3-A6 (fig. 58b). Larvae of both species feed on members of the Fabaceae but larvae of *H. ceraunus* also utilize *Eriogonum* (Polygonaceae). The ground color may be green, red, brownish, or yellow; markings may be absent but often there is a reddish middorsal line and red or yellow lateral lines and dorsolateral chevrons (fig. 74-9c).

Icaricia

There are five species of *Icaricia* in California. They all have a few dendritic setae near the A1 spiracles and lateral margins of the honey gland, moderately stellate chalazae, and flagelliform sensory setae. The number and relative size of prominent setae on the prothoracic shield,

dorsally on T2-A6, laterally on all segments, and subdorsally on T2-A7 differs in each species. In all but *I. icarioides* the prominent dorsal setae are somewhat curved or inclined posteriorly. Other dorsal and lateral setae are tapered to blunt, erect to recurved and may be bent parallel to the body surface. Nondendritic dorsal setae on A7 and A8 are usually somewhat clavate and may be bent parallel to the body surface. *Icaricia acmon* is multivoltine and *I. neurona* is partially bi- or trivoltine; the other *Icaricia* species are univoltine. Diapause occurs in the egg for *I. shasta*, but in the second instar for the other species.

Three species (*I. acmon, I. lupini,* and *I. neurona*) constitute the *I. acmon* species group. Morphological differences in larvae of these species are slight; they are best distinguished according to host plant, locality, and season. The following character discussion is based on populations in the San Bernardino Mountains and does not necessarily apply to populations elsewhere. The length and abundance of prominent setae are generally greatest in *I. neurona* and least in *I. lupini*, thus affording some utility in species identification. Another distinguishing feature concerns the subdorsal prominent setae on A7 (ca midway between the honey gland and spiracles); in *I. neurona* these are well developed, while in *I. lupini* they are usually absent, and in *I. acmon* they are usually present but weakly differentiated from surrounding setae. Dorsal setae on A7 and A8 are semi-erect to strongly bent, (often parallel to the body) weakly tapered to clavate, and mostly apically blunt. Larval ground color is dark green in *I. lupini*, gray-green to dull pinkish gray in *I. neurona*, and highly variable (including green, cream, and maroon) in *I. acmon*. All three species may have a white or yellow lateral line, which in *I. acmon* may be bordered with red. The latter species may also have a contrastingly colored middorsal line and lateral chevrons.

Icaricia acmon, the most common and widespread species, occurs from early spring to fall in all habitats except the open desert; larvae feed on several species of *Eriogonum* and *Lotus*. *Icaricia lupini* is also widespread and utilizes *Eriogonum* as a larval host but is restricted to montane and foothill habitats; in southern California its host is *Eriogonum fasciculatum*, but elsewhere *E. umbellatum* is the major host. *Icaricia neurona* is restricted to montane habitats (usually above 2000m) from the southern Sierra Nevada to the San Bernardino Mountains; hosts are various cespitose *Eriogonum* species, especially *E. kennedyi* and *E. wrightii*.

Larvae of *I. shasta* are similar in appearance to larvae of the previous three species, but differ primarily in the greater development of prominent setae. They differ from all other *Icaricia* in having dark legs and dark chalazae on the prothoracic shield. The ground color is brown to maroon and there are yellowish dorsolateral chevrons and lateral lines (fig. 74-9d); the dorsolateral chevrons may be so enlarged that the ground color is reduced to a narrow line middorsally. They feed on

several cespitose *Astragalus* and *Lupinus* species mostly above 3000m in the Cascade, Sierra Nevada, Warner, and White Mountains.

Icaricia icarioides is a widespread species with various populations occupying habitats from sea level to over 3000m. Larvae feed on perennial lupines and range in ground color from green to pinkish grey. Larval setation differs substantially from that of the other *Icaricia* species; nearly all dorsal and lateral setae on T2-A6 are erect, acutely tapered, straight, and no longer than the spiracle width. Sensory setae are ca 4X as long as other setae on the prothoracic shield and slightly longer than the prominent dorsal setae on T2. Dorsal prominent setae on T3-A6 are no more than ca 1.5X as long as the spiracle width and may be weakly differentiated from other dorsal setae on those segments.

Leptotes

Only one species, *L. marina*, occurs in California. It is multivoltine and abundant throughout southern California, but less common in the Central Valley and uncommon or absent in the central and northern regions of the state. Larval hosts are primarily various Fabaceae and *Plumbago* (Plumbaginaceae), a common ornamental which probably accounts for the success of this species in urban areas; *Adenostoma fasciculatum* (Rosaceae) is also rarely used. The ground color is variable, ranging from pink to green and brownish violet. In general appearance the larvae appear most similar to those of *C. argiolus*. They have apically spatulate sensory setae and are covered with short erect setae arising from strongly stellate chalazae (the lateral points of adjacent chalazae may interdigitate) (fig. 2e); dorsal prominent setae occur on T2 and occasionally on other segments. Larvae of *L. marina* are uniquely distinguishable (among California lycaenids) by the presence of numerous broadly recurved and finely tapered setae (fig. 2b) dorsally and along the lateral fold, intermixed with shorter erect or only slightly bent setae. Similar recurved setae occur in *L. cassius* (Downey and Allyn, 1979) from Florida and in *Syntarucus plinius* from the Australasian region.

Lycaeides

Two species of *Lycaeides* occur in California. *Lycaeides melissa* ranges throughout the state (except the Colorado and Mojave deserts) from near sea level to over 3000m, while *L. idas* occurs primarily above 2000m in the Cascade, central and northern Sierra Nevada, Siskiyou, and Warner Mountains. Larval ground color is green (fig. 74-10a); although some larvae have whitish middorsal and lateral lines and dorsolateral chevrons, others are unmarked. Host plants are herbaceous Fabaceae including *Astragalus, Lotus*, and *Lupinus*. Lowland populations of *L. melissa* are multivoltine while montane populations above 2000m of both species are probably univoltine; diapause occurs as ova.

Physical distinctions between larvae of these species in California are subtle and they are best distinguished by locality. The sensory setae are tapered while dorsal and lateral prominent setae on T2-A6 are ca 3-4X as long as the spiracle width. Other dorsal and dorsolateral setae on T2-A6 are erect, ca as long as the spiracle width, tapered, and arise from moderately stellate chalazae. Typically they have 10-40 dendritic setae per segment near or in the latitude of the spiracles on T3-A2 and A6-A8; fewer dendritic setae may also be present laterally on T1 and T2. Other dorsal setae on A7 and A8 are erect and clavate-capitate, not strongly curved or bent.

Lycaeides larvae from near Mono Lake and the Warner Mountains differ from other populations examined. Their dendritic setae are difficult to observe since they are much smaller and number 0-8 per segment. Most nonprominent dorsal and subdorsal abdominal setae are truncate and sometimes peg-like; some, especially near the honey gland, may be sharply bent near the apex, resembling a railroad spike.

Philotes

There is one species of *Philotes, P. sonorensis,* which occurs throughout cismontane southern California (mostly below 2000m) and northward approximately to the latitude of San Francisco. This insect is univoltine with pupal diapause and flies in late winter and spring; larvae feed on *Dudleya* (Crassulaceae). Ground color ranges from pale green to pink and there are no contrasting markings (fig. 74-10b). Prominent dorsal setae occur only on T2; other dorsal and lateral setae on T2-A6 are erect, straight, weakly tapered to truncate, and ca .5-.7X as long as the spiracle width. Dendritic setae at the margins of the honey gland are clavate, longer than the spiracle width, and appear velvety due to numerous unusually short spicules (fig. 17). Other dorsal setae on A7 and A8 are clavate to strongly capitate (fig. 25) and mostly less than half as long as the spiracle width. The spiracles are brown and the proleg spatulate lobes are small and knob-like.

Philotiella

This genus is closely related to *Euphilotes* and contains a single species, *P. speciosa,* which is nearly confined to the southeastern desert areas of California. The rare subspecies, *P. s. bohartorum* (Shields), occurs in the western foothills of the Sierra Nevada. This species in univoltine with pupal diapause and flies in spring; larval hosts include *Eriogonum reniforme* and *Oxytheca,* especially *O. perfoliata* (Polygonaceae). The larval ground color is green or yellowish and there may be reddish middorsal and lateral lines and dorsolateral chevrons (fig. 74-10c). This species was long included in the genus *Philotes* along with all members of *Euphilotes.* The larvae of *P. speciosa* are most similar to those of *E. mojave* in general appearance; they differ in having virtually

nonstellate chalazae, lighter head pigmentation, and more erect setae. They also differ from larvae of all other California polyommatines except, *A. franklinii*, in lacking eversible tubercles.

Plebejus

There is one California species of *Plebejus*, *P. saepiolus*, which occurs generally above 2000m from Riverside County northward. It is univoltine with diapause in the second instar; larvae feed on *Trifolium* (Fabaceae). The larva is green and often has a white lateral line. In many respects the larvae of this species are similar to those of *Icaricia*. They differ in having dendritic setae on A7 extending from the honey gland laterally to the spiracles, whereas in *Icaricia* the dendritic setae on A7 are confined to the margin of the honey gland. They also differ from all *Icaricia* except, *I. shasta*, in having dark legs.

Plebulina

The single species of *Plebulina*, *P. emigdionis*, occurs only in a few scattered colonies in and around the western Mojave Desert. It is partially bi- or trivoltine and larvae feed on *Atriplex canescens* (Chenopodiaceae). This is the most distinctive California member of the Polyommatinae in terms of biology and larval morphology. It is the only one whose larvae lack a spatulate lobe on the prolegs, have more than four instars (5-7), and are restricted to a single host plant species. Also, the chalazae appear buttressed rather than stellate; but, unlike the buttressed chalazae of thecline larvae, the lateral ridges do not appear to be basally fused with the cuticle. Dendritic setae are few in number and confined to the vicinity of the A1 spiracles and margin of the honey gland; they and most other dorsal and lateral setae on T2-A6 are erect, tapered, and ca half as long as the spiracle width. A pair of prominent dorsal setae on T2 are ca 6X as long as the spiracle width. As with many other polyommatine larvae, most dorsal setae on A7 and A8 are clavate and strongly bent or recumbent. Lenticles are dark brown in contrast to most chalazae which are nonpigmented. The sensory setae are filiform. Larvae are grayish pink or green and lack contrasting markings (fig. 74-10d). They probably feed nocturnally; during the day they can be found at the base of the host plant in the company of ants.

Literature Cited

ACKERY, P. R., 1984. Systematic and faunistic studies on butterflies. Symp. Roy. Ent. Soc. Lond. 11:9-21.

BETHUNE-BAKER, G. T., 1925. A revision of the Liphyrinae together with a description of the structure of the puparium of *Liphyra brassolis* and of the pupae of *Aslauga vininga* and *A. lamborni* (Lepidoptera). Trans. Ent. Soc. Lond. 1924: 199-238, 25 pls.

BOURQUIN, F., 1953. Notas sobre la metamorphosis de *Hamearis susanae* Orfila, 1953 con oruga mirmecófila. Rev. Soc. Ento. Argen. 16:83-87.

BRUCH, C., 1926. Orugas mirmecofilas de *Hamearis epulus signatus* Stich. Rev. Soc. Ento. Argen. 1:1-9.

CLARK, G. C. & C. G. C. DICKSON, 1956a. The honey gland and tubercles of the Lycaenidae. Lep. News 10:37-43.

———, 1956b. Proposed classification of South African Lycaenidae from the early stages. J. Ent. Soc. Sth. Africa 10:195-215

———, 1971. *Life Histories of the South African Lycaenid Butterflies*. Purnell, Capetown. 272pp.

CLENCH, H. K. 1961. Tribe Theclini in Ehrlich, P. R. and A. H. Ehrlich, *How to Know the Butterflies*. W. C. Brown Co., Dubuque. pp.209-210.

COMSTOCK, J. A., 1928. Studies in Pacific Coast Lepidoptera. Bull. So. Cal. Acad. Sci. 27:80-89.

———, 1930. Metamorphoses of five California diurnals (Lepidoptera). Bull. So. Cal. Acad. Sci. 31:33-45.

COMSTOCK, J. A. & C. M. DAMMERS, 1932. Early stages of *Melitaea leanira wrightii* and *Calephelis nemesis*. Bull. So. Cal. Acad. Sci. 31:9-15.

COTTRELL, C. B., 1984. Aphytophagy in butterflies: its relationship to myrmecophily. Zool. J. Lin. Soc. 80:1-57.

DEVRIES, P. J., 1984. Of crazy ants and Curetinae: are *Curetis* butterflies tended by ants? Zool. J. Lin. Soc. 80:59-66.

DEVRIES, P. J., D. J. HARVEY & I. J. KITCHING, 1986. The ant associated organs on the larva of the lycaenid butterfly *Curetis regula* Evans. J. Nat. Hist 20:621-633.

DOS PASSOS, C. F., 1936. The life history of Calephelis borealis (Lepidoptera). Can. Ent. 68:166-170.

DOWNEY, J. C., 1987. Family Lycaenidae in Stehr, F. W., *Immature Insects*. Kendall/Hunt Co., Dubuque. pp.443-446.

DOWNEY, J. C. & A. C. ALLYN, 1979. Morphology and biology of the immature stages of *Leptotes cassius theonus* (Lucas) (Lepid.: Lycaenidae). Bull. Allyn Mus. 55:1-27.

———, 1984. Chaetotaxy of the first instar larva of *Hemiargus ceraunus antibubastus* (Hbn.) (Lycaenidae). Bull. Allyn Mus. 90:1-4.

EHRLICH, P.R., 1958. The comparative morphology, phylogeny and higher classification of the butterflies. (Lepidoptera: Papilionoidea). Kans. Univ. Sci. Bull. 39:305-370.

ELIOT, J. N., 1973. The higher classification of the Lycaenidae (Lepidoptera): a tentative arrangement. Bull. Brit. Mus. (Nat. Hist.) Ent. 28:371-505.

EMMEL, T. C. & J. F. EMMEL, 1973. The butterflies of southern California. Natural History Museum of Los Angeles County, Science Series 26:1-148.

FERRIS, C. D., 1974. Distribution of arctic-alpine *Lycaena phlaeas* L. (Lycaenidae) in North America with designation of a new subspecies. Bull. Allyn Mus. 18:1-13.

FRANZL, S., M. LOCKE, & P. HUIE, 1984. Lenticles: innervated secretory structures that are expressed at every other moult. Tissue and Cell 16:251-268.

GORELICK, G. A., 1971. A biosystematic study of two species of Callophrys (Callophrys) in California (Lycaenidae). J. Lep. Soc. 25 (supl. 2):1-41.

————, 1987. Santa Catalina Island's endemic Lepidoptera III. The Avalon hairstreak, Strymon avalona (Lycaenidae): an ecological study. Atala 14(1):1-12.

HARVEY, D. J., 1987. Family Riodinidae in Stehr, F. W., Immature Insects. Kendall/Hunt Co., Dubuque. pp.446-447.

HENNING, S. F., 1983a. Biological groups within the Lycaenidae (Lepidoptera). J. Ent. Soc. Sth. Afr. 46:65-85.

————, 1983b. Chemical communication between lycaenid larvae (Lepidoptera: Lycaenidae) and ants (Hymenoptera: Formicidae). J. Ent. Soc. Sth. Afr. 46:341-366.

HINTON, H. E., 1946. On the homology and nomenclature of setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. Trans. Roy. Ent. Soc. Lond. 97:1-37.

————, 1951. Myrmecophilous Lycaenidae and other Lepidoptera — a summary. Trans. S. Lond. Ent. Nat. Hist. Soc. 1949-50:111-175.

JOHNSON, J. M., 1981. Unusual food plant. Utahensis 1:10.

JOHNSON, K., 1978. Specificity, geographic distributions, and foodplant diversity in four Callophrys (Mitoura) (Lycaenidae). J. Lep. Soc. 32:3-19.

JOHNSON, K. & G. BALOGH, 1977. Studies in the Lycaeninae (Lycaenidae) 2. taxonomy and evolution of the Nearctic Lycaena rubidus Complex, with description of a new species. Bull, Allyn Mus. 43:1-62.

KENDALL, R. O., 1976. Larval foodplants and life history notes for some metal-marks (Lepidoptera: Riodinidae) from Mexico and Texas. Bull Allyn Mus. 32:1-12.

KITCHING, R. L., 1983. Myrmecophilous organs of the larvae and pupae of the lycaenid butterfly, Jalmenus evagoras (Donovan). J. Nat. Hist. 17:471-81.

————, and B. Luke, 1985. The myrmecophilous organs of the larvae of some British Lycaenidae (Lepidoptera): a comparative study. J. Nat. Hist. 19: 259-76.

LANGSTON, R. L. & J. A. COMSTOCK, 1966. Life history of Philotes enoptes bayensis (Lepidoptera: Lycaenidae). Pan Pac. Ent. 42:102-108.

LAWRENCE, D. A. & J. C. DOWNEY, 1966. Morphology of the immature stages of Everes comyntas Godart (Lycaenidae). J. Res. Lepid. 5:61-96.

MALICKY, H., 1969a. Versuch einer analyse der Ökologischen Beziehungen zwischen Lycaeniden (Lepidoptera) und Formiciden (Hymenoptera). Tijd. Ent. 112:213-98.

————, 1969b. Uebersicht ueber Präimaginal stadien, Bionomie and Ökologie der mitteleuropäischen Lycaenidae (Lepidoptera). Mitt. Ent. Gesell. Basel 2/3:25-91.

————, 1970. New aspects on the association between lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). J. Lep. Soc. 24:191-202.

MASCHWITZ, U., M. WUST & K. SCHURIAN, 1975. Blaulingsraupen als zuckerlieferanten für Ameisen. Oecologia (Berlin) 18:17-21.

MCALPINE, W. S., 1938. Life history of Calephelis muticum (McAlpine): Lepidoptera. Bull. Brooklyn Ent. Soc. 33:111-121.

MILLER, L. D. & F. M. BROWN, 1979. Studies in the Lycaeninae (Lycaenidae) 4. The higher classification of the American coppers. Bull. Allyn Mus. 51:1-30.

————, 1981. A catalogue/checklist of the butterflies of America north of Mexico. Lepid. Soc. Memoir No. 2.

MUNZ, P. A. & D. D. KECK, 1959. *A California Flora*. University of California Press, Berkeley and Los Angeles. 1681pp.

ORSAK, O. & D. W. WHITMAN, 1987. Chromatic polymorphism in *Callophrys mossii bayensis* larvae (Lycaenidae): spectral characterization, short-term color shifts, and natural morph frequencies. J. Res. Lepid. 25:188-201.

PETERSON, A., 1948. *Larvae of Insects Part I Lepidoptera and Hymenoptera*. Edwards Bros., Inc. Ann Arbor, Michigan. 315pp.

PIERCE, N. E. & P. S. MEAD, 1981. Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. Science 211:1185-1187.

PIERCE, N. E., 1983. The ecology and evolution of symbioses between lycaenid butterflies and ants. Ph. D. dissertation, Harvard University, Cambridge, Mass.

POWELL, J. A., 1968. Foodplants of *Callophrys (Incisalia) iroides*. J. Lep. Soc. 22:225-226.

PRATT, G. F. & G. R. BALLMER, 1986. Clarification of the larval host plant of *Epidemia mariposa* (Lycaenidae) in northern California. J. Lep. Soc. 40:127.

————, 1987. The phenetics and comparative biology of *Euphilotes enoptes* (Boisduval) (Lycaenidae) from the San Bernardino Mountains. J. Res. Lepid. 25:121-135.

PYLE, R. M., 1981. *The Audubon Society Field Guide to North American Butter-flies*. Chanticleer Press, A. A. Knopf, New York. 916pp.

ROSS, G. N., 1964. Life history studies on Mexican butterflies II. Early stages of *Anatole rossi* a new myrmecophilous metalmark. J. Res. Lepid. 3:81-94.

SCOTT, J. A., 1980. Geographic variation in *Lycaena xanthoides*. J. Res. Lep. 18:50-59.

————, 1986. *The butterflies of North America a natural history and field guide*. Stanford University Press, Stanford California. 583pp.

SHAPIRO, A. M., 1974. A salt-marsh population of *Lycaena helloides* (Lepidoptera: Lycaenidae) feeding on *Potentilla* (Rosaceae). Ent. News 85: 40-44.

SHIELDS, O. A., 1984. Comments on recent papers regarding western Cupres-saceae — feeding *Callophrys (Mitoura)*. Utahensis 4:51-56.

STEHR, F. W., 1987. *Immature Insects*. Kendall/Hunt Co., Dubuque. 754pp.

VANE-WRIGHT, R.I., 1978. Ecological and behavioral origins of diversity in butterflies. Symp. Roy. Ent. Soc. Lond. 9:56-70.

WEBSTER, R. P. & M. C. NIELSEN, 1984. Myrmecophily in the Edward's hairstreak butterfly *Satyrium edwardsii* (Lycaenidae). J. Lepid. Soc. 38:124-133.

WRIGHT, D. M., 1983. Life history and morphology of the immature stages of the bog copper butterfly *Lycaena epixanthe* (Bsd. & Le C.). J. Res. Lepid. 22:47-100.

GLOSSARY

A1, A2, A3,...A10: Abdominal segments 1, 2, 3,...10.

Adfrontal sutures: A pair of sutures extending dorsally from the anterior mandibular articulations and converging at the stem of the epicranial (or coronal) suture. In many Lepidoptera (but not Lycaenidae) two pairs of roughly parallel sutures extend from the coronal suture to the mandibular articulations, the more mesal frontal sutures and lateral to them the adfrontal sutures.

Allopatric: Occurring in different areas; usually pertaining to species or subspecies whose ranges do not overlap.

Anal: Pertaining to the last adbominal segment.

Anal prolegs: The terminal pair of prolegs on abdominal segment 10.

Biordinal: Two sizes, as in two lengths of crochets arising from a single line.

Bivoltine: Having two generations per year.

Buttressed chalazae: Chalazae with vertical lateral ridges which fuse distally with the cuticle, appearing buttressed (fig. 2n).

Ca: About or approximately.

Capitate: Abruptly enlarged distally, especially pertaining to setae.

Caudad: In the direction of the anal or tail end; posterior.

Cephalad: In the direction of the head; anterior.

Cephalic: Pertaining to the head.

Chaetotaxy: The arrangement or distribution of setae.

Chalaza(ae): A sclerotized basal papilla from which a seta arises.

Clavate: Club-shaped; more-or-less cylindric and gradually enlarged distally, especially pertaining to setae.

Coxa(ae): The basal segment of a true leg.

Crochet(s): A hooklike sclerotized structure at the distal end of a proleg, usually with many others arranged in rows.

Cylindric: Circular in cross-section, especially pertaining to setae.

Dendritic seta(ae): A specialized seta (usually) with relatively long, fine lateral spicules and often occurring in close proximity to the honey gland and spiracles (figs. 15-18).

Distal: Toward the end of an appendage farthest from its attachment.

Dorsal: Toward or pertaining to the dorsum.

Dorsal line: A longitudinal line along the dorsum, often apparent as a contrasting color with respect to the ground color.

Dorsum: The top of a larva when resting on a substrate; the side opposite its legs.

Echinoid seta(ae): Short globular setae with stout, apically flared processes found in *Calephelis* larvae (fig. 31).

Epicranial suture: A 'Y'-shaped suture separating left and right halves of the cranium which is forked anteriorly.

Eversible tubercle(s): A fleshy tubercle in many lycaenid larvae, located slightly posterolateral to the spiracle on abdominal segment 8, which is normally retracted and not visible.

Filiform: Filamentous or thread-like; slender, long, and little or not at all tapered, especially pertaining to setae.

Flagelliform: Whip-like; slender and finely tapered, especially pertaining to setae.

Frons: That portion of the head between the anterior arms of the epicranial suture (adfrontal or frontal sutures) and immediately above the clypeus.

Frontal sutures: The anterior arms of the epicranial suture which terminate at the anterior mandibular articulations and form the lateral margins of the frons. In lycaenid larvae these are also known as adfrontal sutures.

Ground color: The primary color of a larva on which a pattern of contrasting color(s) may be superimposed.

Honey gland: A partly eversible transverse middorsal gland on abdominal segment 7.

Instar: The stage between larval molts; the first instar emerges from an ovum; the last instar immediately precedes the pupal stage.

Lateral: Pertaining to the sides.

Lateral fold: A fleshy cuticular fold below the spiracles extending posteriorly from T1.

Lateral line: A longitudinal line of contrasting color coinciding with the lateral fold.

Lateral spicule: A small filamentous or spine-like lateral process of a seta.

Lenticle: A small cuticular lens-like structure, surmounting or set into a short chalaza-like collar, found in hesperiids and lycaenids.

Mesoseries: A band of crochets along the mesal side of a proleg.

Mesothorax: The second segment of the thorax, bearing the second pair true legs.

Metathorax: The third segment of the thorax, bearing the third pair of ture legs.

Middorsal: Located along the dorsal midline.

Multivoltine: Having several (continous) generations per year.

Mushroom lenticle: A stalked lenticle, narrowest at the base, found in *Atlides halesus* (fig. 26).

Mushroom seta(e): A short, stout, multibranched seta, resembling a mushroom when viewed under low magnification, found in the Lycaeninae (figs. 2q, 22).

Neck setae: Short, stout, tooth-like setae on the neck area of lycaenid larvae (fig. 27).

O1, O2, O3,...O6: Ocelli 1-6; numbered as in fig. 68.

Ocellus(i): One of six simple eyes or stemmata located on each side of the head of Lepidoptera larvae (fig. 68).

Onisciform: Somewhat spindle-shaped but ventrally flattened, as in the sow bug (*Oniscus*).

Papilla(ae): A small cuticular projection or elevation.

Pheromone: A chemical used by an organism to communicate with another member of its species.

Planta: The distal end of the proleg to which the crochets are attached.

Plumose seta(e): A type of seta (usually very long and filamentous) found in *Apodemia* and *Calephelis* larvae which has numerous short, fine lateral processes (figs. 31, 32).

Polymorphic: Having several forms or color patterns.

Posterior: Caudad.

Primary seta(e): Setae representing the archetypal setation of the Lepidoptera, occurring in fixed numbers and locations in many lepidopterous families but only in first instars of Lycaenidae.

Proleg: A fleshy appendage with distal crochets occurring in pairs ventrally on the abdominal segments.

Prominence: A fleshy elevation of the body surface.

Prominent seta(e): Setae occurring in locations typical for primary setae and which are distinguishable from surrounding secondary seta by their greater length and/or erectness; in some cases these may be primary setae but often they exceed the basic number of primary setae in a given location.

Pupa: The resting stage intermediate between the mature larva and adult in holometabolous insects.

Reclinate: Lying against or at a low angle to the body surface, especially pertaining to setae which are not bent near the base.

Recumbent: Lying down or reclining against the cuticle, especially pertaining to setae strongly bent near the base.

Recurved: Broadly bent back toward the base, especially pertaining to setae.

Retractile: Retractable; able to be withdrawn, as with the head of many lycaenid larvae.

Sclerite: A hardened (sclerotized) part of the body wall.

Secondary seta(e): Those setae occurring in addition to the basic complement of primary setae in larvae of lycaenids and many other lepidopterous families.

Semiochemical: Chemicals produced by one organism that incite response in other organisms.

Sensory seta(e): A specialized pair of setae located anterodorsal to the prothoracic spiracles; in lycaenid larvae they are on the prothoracic shield, near its lateral margins.

Seta(e): A sclerotized hair or bristle surrounded basally by a small cuticular ring and often arising from a chalazae.

Spatulate: Enlarged and compressed or flattened distally, as in a spatula, especially pertaining to setae.

Spatulate lobe: A fleshy lobe (usually distally flared and flattened) arising near the center of the mesoseries of crochets on most lycaenid larvae.

Spicule: A spine-like projection.

Spinule: A short sclerotized cuticular projection.

Spiracle: A sclerotized, cuticular pore associated with internal tracheae, a pair of which are located laterally on the prothorax and abdominal segments 1-8.

Stellate chalaza: A chalaza with distal or lateral pointed projections.

Stemma(ta): One of a group of lateral ocelli found in lepidopterous larvae; ocellus.

Subdorsal: Located slightly lateral to the dorsal midline, intermediate between the dorsal and lateral regions.

Subprimary seta(e): Those setae (additional to primary setae) occurring in fixed locations typical of some families.

Suture: A seam where two sclerites join.

Sympatric: Occurring in the same area.

T1, T2, T3: Referring to the prothorax, mesothorax, and metathorax, respectively.

Tapered: Becoming gradually narrower distally, especially pertaining to setae.

Triordinal: Pertaining to crochets of three lengths arising from a single row.

Taxon(a): A taxonomic unit such as species, genus, family, etc.

Uniordinal: Pertaining to crochets of a single length arising from a single line.

Ventral: Pertaining to the lower side of a larva when resting on the substrate; the side from which the legs and prolegs arise.

Ventral prothoracic gland: An eversible gland arising midventrally anterior to the prothoracic legs of some Lepidoptera larvae.

Verruca(e): A distinctly bounded (often sclerotized, pigmented, or raised) area from which several setae arise.

Appendix 1. List of the Lycaenidae of California

Riodininiae:
Apodemia mormo (C. and R. Felder, 1859)
    "   *palmerii* (W. H. Edwards, 1870)
Calephelis nemesis (W. H. Edwards, 1871)
    "   *wrighti* Holland, 1930
Lycaeninae:
Lycaena arota (Boisduval, 1852)
    "   *cupreus* (W. H. Edwards, 1870)
    "   *editha* (Mead, 1878)
    "   *gorgon* (Boisduval, 1852)
    "   *helloides* (Boisduval, 1852)
    "   *hermes* (W. H. Edwards, 1870)
    "   *heteronea* (Boisduval, 1852)
    "   *mariposa* (Reakirt, 1866)
    "   *nivalis* (Boisduval, 1869)
    "   *phlaeas* (Linnaeus, 1761)
    "   *rubidus* (Behr, 1866)
    "   *xanthoides* (Boisduval, 1852)
Theclinae:
Atlides halesus (Cramer, 1777)
Callophrys (Callophrys) comstocki Henne, 1940
    "   "   *dumetorum* (Boisduval, 1852)
    "   "   *lemberti* Tilden, 1963
    "   "   *perplexa* Barnes and Benjamin, 1923
    " *(Incisalia)* *augustus* (W. Kirby, 1837)
    "   "   *eryphon* (Boisduval, 1852)
    "   "   *fotis* (Strecker, 1878)
    "   "   *mossii* (Hy. Edwards, 1881)
    " (Mitoura) *johnsoni* (Skinner, 1904)
    "   "   *loki* (Skinner, 1907)
    "   "   *nelsoni* (Boisduval, 1869)
    "   "   *siva* (W. H. Edwards, 1874)
    "   "   *spinetorum* (Hewitson, 1867)
    "   "   *thornei* (Brown, 1983)
Habrodais grunus (Boisduval, 1852)
Harkenclenus titus (Fabricius, 1793)
Ministrymon leda (W. H. Edwards, 1882)
Satyrium auretorum (Boisduval, 1852)
Satyrium behrii (W. H. Edwards, 1870)
    "   *californica* (W. H. Edwards, 1862)
    "   *fuliginosum* (W. H. Edwards, 1861)
    "   *saepium* (Boisduval, 1852)
    "   *sylvinus* (Boisduval, 1852)
    "   *tetra* (W. H. Edwards, 1870)
Strymon avalona (W. G. Wright, 1905)
    "   *columella* (Fabricius, 1793)
    "   *melinus* Hübner, 1818

Polyommatinae:
Agriades franklinii (Curtis, 1835)
Brephidium exilis (Boisduval, 1852)
Celastrina argiolus (Linnaeus, 1758)
Everes amyntula (Boisduval, 1852)
   "   *comyntas* (Godart, 1824)
Euphilotes battoides (Behr, 1867)
      "   *enoptes* (Boisduval, 1852)
      "   *mojave* (Watson and W. P. Comstock, 1920)
      "   *rita* (Barnes and McDunnough, 1916)
Glaucopsyche lygdamus (Doubleday, 1841)
     "   *piasus* (Boisduval, 1852)
Hemiargus ceraunus (Fabricius, 1793)
    "   *isola* (Reakirt, 1866)
Icarica acmon (Westwood and Hewitson, 1852)
  "   *icarioides* (Boisduval, 1852)
  "   *lupini* (Boisduval, 1869)
  "   *neurona* (Skinner, 1902)
  "   *shasta* (W. H. Edwards, 1862)
Leptotes marina (Reakirt, 1860)
Lycaeides idas (Linnaeus, 1761)
    "   *melissa* (W. H. Edwards, 1873)
Philotes sonorensis (C. and R. Felder, 1865)
Philotiella speciosa (Hy. Edwards, 1867)
Plebejus saepiolus (Boisduval, 1852)
Plebulina emigdionis (F. Grinnell, 1905)

Appendix 2.   New and reconfirmed larval host plants.

Host species	Butterfly species

AIZOACEAE
Sesuvium verrucosum Raf.   *B. exilis*

ASTERACEAE
Baccharis glutinosa Pers.   *C. nemesis, C. argiolus*
Bebbia juncea (Benth.) Greene   *C. wrighti*
Helianthus annuus L. ssp. *lenticularis*   *S. melinus*
    (Dougl.) Ckll.

CHENOPODIACEAE
Atriplex canescens (Pursh) Nutt.   *B. exilis, P. emigdionis*
    "   *semibaccata* R. Br.   *B. exilis*
Chenopodium sp.   *B. exilis*
Salsola iberica Sennen & Pau.   *B. exilis*
Suaeda moquinii (Torr.) Greene   *B. exilis*

CONVOLVULACEAE
Cuscuta sp.   *C. (I.) augustus*

CRASSULACEAE
Dudleya abramsii Rose   *P. sonorensis*
    "   *cymosa* (Lem.) Britt. & Rose   *P. sonorensis*
    "   *lanceolata* (Nutt.) Britt. & Rose   *P. sonorensis, S. melinus*
    "   *saxosa* (Jones) Britt. & Rose   *P. sonorensis, S. melinus*
Sedum spathulifolium Hook.   *C. (I.) mossii*

CUPRESSACEAE
Juniperus californica Carr.   *C. (M.) loki, C. (M.) siva*

ERICACEAE
Vaccinium arbuscula (Gray) Merriam   *L. mariposa*
    "   *myrtillus* L.   *L. mariposa* (Oregon record)

FABACEAE
Amorpha californica Nutt.   *L. marina, S. melinus*
    "   *fruticosa* L. var. *occidentalis*   *L. marina*
            (Abrams) Kearn. & Peeb.
Astragalus canadensis L. var. *brevidens*   *L. melissa*
            (Gand.) Barneby
    "   *douglasii* (T. & G.) Gray   *E. amyntula, H. ceraunus, L.*
                                                  melissa
    "   *lentiginosus* Dougl.   *E. amyntula, G. lygdamus,*
                                                  L. melissa
    "   *palmeri* Gray   *E. amyntula, H. ceraunus*
    "   *whitneyi* Gray   *E. amyntula*
Calliandra eriophylla Benth.   *L. marina*
Dalea searalsiae (Gray) Barneby   *H. isola*

Hoffmannseggia microphylla Torr. — *H. ceraunus*

Lotus argophyllus (Gray) Greene — *S. avalona, C. perplexa*

    "   *crassifolius* (Benth.) Greene — *C. perplexa, S. melinus*

    "   *humistratus* Greene — *G. lygdamus* (Oregon record)

    "   *nevadensis* Greene — *I. acmon*

    "   *oblongifolius* (Benth.) Green — *L. idas*

    "   *purshianus* (Benth.) Clem. & Clem. — *I. acmon, L. melissa*

    "   *procumbens* (Greene) Greene — *G. lygdamus, L. marina*

    "   *rigidus* (Benth.) Greene — *G. lygdamus*

    "   *scoparius* (Nutt. in T. & C.) Ottley — *C. perplexa, G. lgydamus, L. marina, S melinus*

Lupinus andersonii Wats. — *G. piasus, S. fuliginosum*

    "   *argenteus* Pursh var. *tenellus* (Dougl. ex D. Don) D. Dunn — *I. icarioides*

    "   *breweri* Gray — *I. shasta*

    "   *caudatus* Kell. — *G. lygdamus, S. fuliginosum*

    "   *excubitus* Jones — *G. piasus, I. icarioides,*

    "   *latifolius* Agardh — *G. lygdamus, G. piasus, I. acmon, S. melinus*

    "   *magnificus* Jones — *H. isola*

Marina parryi (T. & G.) Barneby — *H. isola*

Medicago sativa L. — *L. marina*

Prosopis glandulosa Torr. — *H. ceraunus, L. marina, M. leda*

    "   *pubescens* Benth. — *A. palmerii*

Trifolium monanthum Gray — *P. saepiolus*

    "   *monoense* Greene — *P. saepiolus*

    "   sp. — *P. saepiolus*

Vicia benghalensis L. — *G. lygdamus*

FAGACEAE

Quercus chrysolepis Liebm. — *H. grunus, S. auretorum*

    "   *cornelius-mulleri* Nixon & Steele — *S. auretorum*

    "   *douglasii* H. & A. — *S. auretorum*

    "   *wislizenii* A. DC. — *S. auretorum, S. californica*

LAMIACEAE

Rosmarinus officionalis L. — *S. melinus*

Mentha piperita L. — *S. melinus*

MALVACEAE

Gossypium hirsutum L. — *S. melinus*

Hibiscus denudatus Benth. — *S. columella, S. melinus*

    "   *rosa-sinensis* L. — *S. melinus*

Sphaeralcea emoryi Torr. in Gray — *S. melinus*

PLUMBAGINACEAE

Plumbago auriculata Lam. — *L. marina*

POLYGONACEAE

Eriogonum	*caespitosum* Nutt.	*I. lupini*
"	*cinereum* Benth.	*E. battoides*
"	*davidsonii* Greene	*E. enoptes, E. rita, H. ceraunus, I. acmon, S. melinus*
"	*deserticola* S. Wats.	*A. mormo*
"	*elatum* Dougl. ex Benth.	*E. enoptes, S. melinus*
"	*elongatum* Benth.	*C. perplexa, E. enoptes, H. ceraunus, I. acmon, L. gorgon, S. melinus*
"	*fasciculatum* Benth.	*A. mormo, C. comstocki, E. battoides, I. acmon, I. lupini, L. heteronea*
"	*heermannii* Dur. & Hilg.	*A. mormo, C. comstocki, E. battoides*
"	*heracleoides* Nutt.	*C. lemberti*
"	*incanum* Torr. & Gray.	*E. battoides, C. lemberti*
"	*inflatum* Torr. & Frem.	*A. mormo, S. melinus*
"	*insigne* Wats.	*A. mormo*
"	*kennedyi* Porter ex Wats.	*C. comstocki, E. battoides, E. enoptes, I. acmon, I. neurona*
"	*latifolium* Sm.	*A. mormo, C. dumetorum, E. enoptes*
"	*lobbii* T. & G.	*E. battoides, I. lupini*
"	*marifolium* T. & G.	*C. lemberti, E. battoides*
"	*microthecum* Nutt.	*C. comstocki, E. battoides, E. rita, S. melinus*
"	*nidularium* Cov.	*C. comstocki*
"	*nudum* Dougl. ex Benth.	*A. mormo, C. lemberti, E. enoptes, I. acmon, L. gorgon, S. melinus*
"	*ovalifolium* Nutt.	*E. battoides, I. acmon, I. lupini*
"	*panamintense* Morton	*E. enoptes*
"	*parvifolium* Sm. in Rees	*E. battoides, E. enoptes, I. acmon, S. melinus*
"	*plumatella* Dur. & Hilg.	*E. enoptes, E. rita, I. acmon, H. ceraunus*
"	*pusillum* T. & G.	*E. mojave*
"	*reniforme* Torr. & Frem.	*E. mojave, H. ceraunus, I. acmon, P. speciosa*
"	*roseum* Dur. & Hilg.	*E. enoptes, E. rita, S. melinus*
"	*thurberi* Torr.	*I. acmon*
"	*umbellatum* Torr.	*A. mormo, C. comstocki, C. lemberti, E. battoides, E. enoptes, I. lupini, I. neurona, L. heteronea*
"	*wrightii* Torr. ex Benth.	*C. argiolus (Arizona record), E. enoptes, H. ceraunus, I. acmon, S. melinus*

Oxyria digyna (L.) Hill   *L. phlaeas*
Oxytheca perfoliata T. & G.   *A. mormo*
Polygonum amphibeum L.   *L. hellodies*
      "   *lapathifolium* L.   *S. melinus*
Rumex angiocarpus Murbeck   *L. editha*
  "   *californicus* Rech.   *L. cupreus*
  "   *crispus* L.   *L. xanthoides*
  "   *paucifolius* Nutt. ex Wats.   *L. cupreus, L. editha*
  "   *salicifolius* Weinm.   *L. editha, L. xanthoides*
  "   *triangulivalvis* (Danser) Rech.   *L. cupreus, L. rubidus*

PRIMULACEAE
Dodecatheon alpinum (Gray) Greene   *A. franklinii*

RHAMNACEAE
Ceanothus cordulatus Kell.   *S. californica, S. saepium*
    "   *cuneatus* (Hook.) Nutt.   *S. saepium*
    "   *crassifolius* Torr.   *S. saepium*
    "   *greggii* Gray var. *perplexans*   *C. (I.) augustus, S. saepium*
      (Trel.) Jeps.
    "   *leucodermis* Greene   *C. (I.) augustus, C. argiolus, S.*
                                         saepium
    "   *oliganthus* Nutt. in T. & G.   *S. saepium*
    "   *palmeri* Trel.   *C. (I.) augustus, C. argiolus*
Rhamnus crocea Nutt. in T. & G.   *C. (I.) augustus, L. hermes*
    "   *ilicifolia* Kell.   *C. (I) augustus*

ROSACEAE
Adenostoma fasciculatum H. & A.   *C. argiolus, C. (I.) augustus, L.*
                                          marina
Cercocarpus betuloides Nutt. ex T. & G.   *S. tetra*
Cowania mexicana D. Don var.   *C. (I.) fotis*
  stansburiana (Torr.) Jeps.
Heteromeles arbutifolia M. Roem.   *C. argiolus, C. (I.) augustus*
Malus sylvestris (L.) P. Mill.   *S. melinus*
Prunus ilicifolia (Nutt.) Walp.   *C. argiolus, C. (I.) augustus*
Purshia glandulosa Curran   *S. behrii*
    "   *tridentata* (Pursh) DC.   *S. behrii*
Rubus ursinus Cham. & Schlecht.   *S. melinus*

SALICACEAE
Salix sp.   *S. melinus*
  "   *hindsiana* Benth.   *S. sylvinus, S. melinus*
  "   *lasiolepis* Benth.   *S. sylvinus*

SAXIFRAGACEAE
Ribes quercetorum Greene   *L. arota*
  "   *roezlii* Regel.   *L. arota*
  "   *velutinum* Greene   *L. arota*

VISCACEAE

Arceuthobium campylopodum Engelm.   *C.(M.) spinetorum*
    in Gray

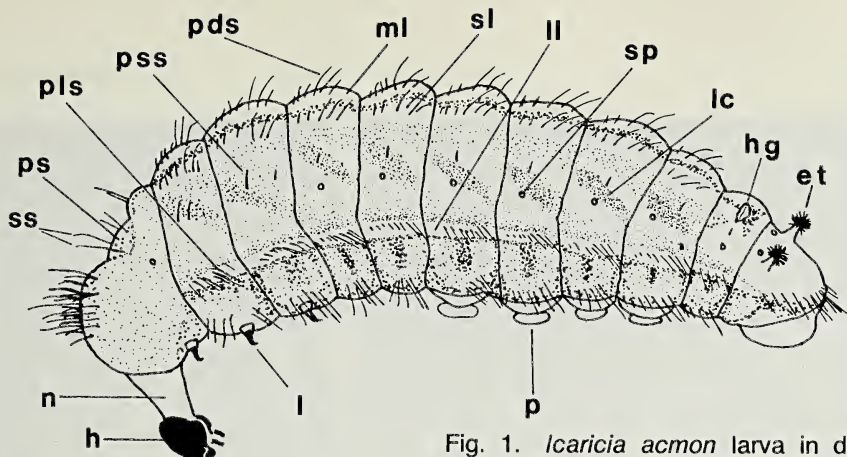*Phoradendron tomentosum* (Englm. ex   *A. halesus*
    Gray)

Fig. 1. *Icaricia acmon* larva in distended condition. Key to abbreviations: et=eversible tubercle, h=head, hg=honey gland, l=leg, lc=lateral chevron, ll=lateral line, ml=middorsal line, n=neck, p=proleg, pds=prominent dorsal setae, pls=prominent lateral setae, ps=prothoracic shield, pss=prominent subdorsal setae, sl=subdorsal line, sp=spiracle, ss=sensory setae.
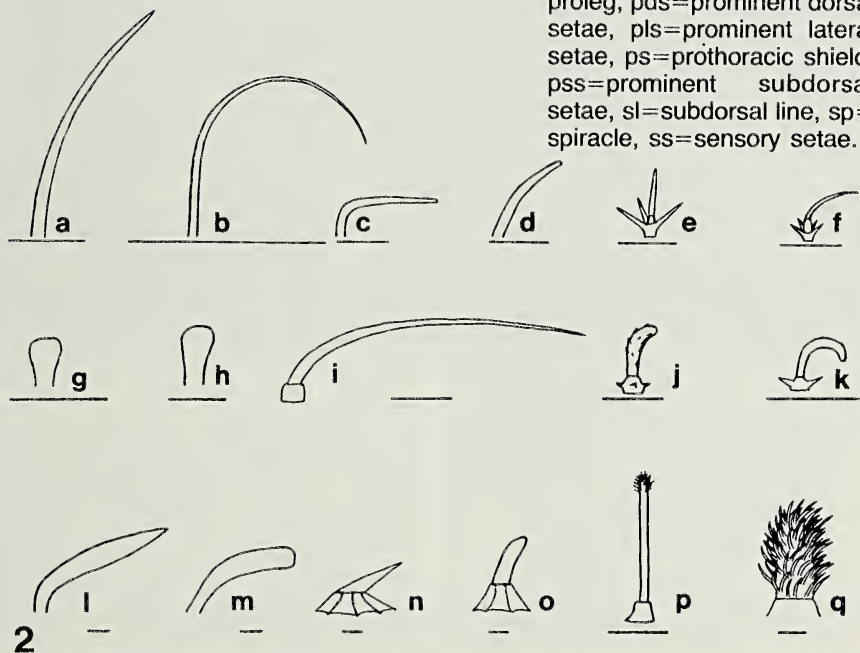
Fig. 2. Some variations in lycaenid setal structure: a) erect, slightly curved prominent seta (*L. nivalis*), b) broadly recurved and finely tapered seta (*L. marina*), c) seta sharply bent near base and apically truncate (*L. nivalis*), d) semierect, apically truncate seta (*L. mariposa*), e) erect, straight seta with stellate chalaza (*L. marina*), f) recurved, apically pointed seta with stellate chalaza (*C. argiolus*), g) clavate-capitate seta (*H. titus*), h) clavate-capitate seta (*L. xanthoides*), i) slender recumbent seta (*L. gorgon*), j) erect, apically bent seta with stellate chalaza (*L. melissa*), k) recurved, apically blunt seta with stellate chalaza (*G. piasus*), l) spindle-shaped, apically pointed seta (*H. ceraunus*), m) clavate, truncate seta (*I. acmon*), n) reclinate seta with buttressed chalaza (*S. california*), o) slightly inclined, blunt seta with buttressed chalaza (*S. fuliginosum*), p) weakly dendritic seta with nonsculptured chalaza (*L. heteronea*), q) mushroom seta with tapered, unbranched processes (*L. arota*). Bar scale=0.1mm for a-k and p and 0.01mm for l-o and q.
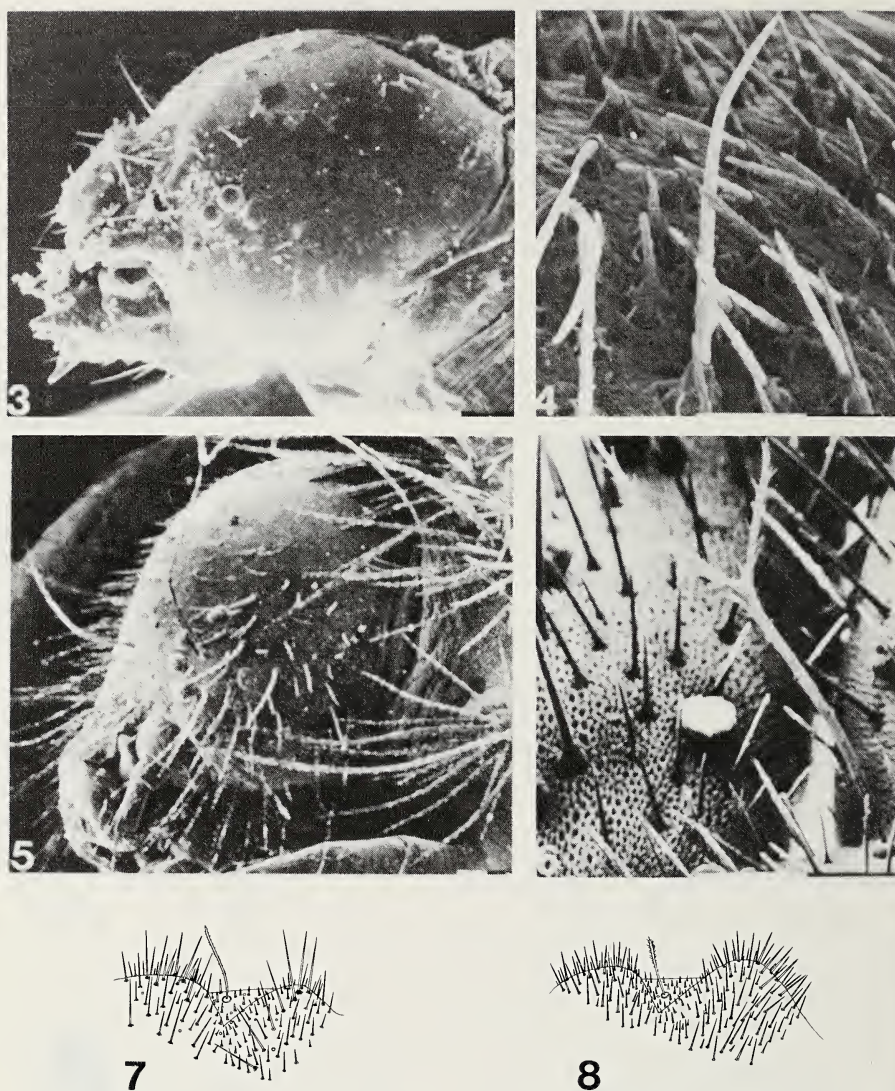
Figs. 3-8.   Some head and body setae. Fig. 3. *Philotiella speciosa* head. Fig. 4.
Prominent seta and other setae on mesothoracic dorsal prominence of
Callophrys (M.) johnsoni. Fig. 5. *Apodemia mormo* head; note long
setae on cranium and anterior margin of prothorax. Fig. 6. Branched
sensory seta on *Atlides halesus*. Fig. 7. Lateral view of prothoracic
dorsum of *Callophrys (C.) perplexa*. Note relatively low dorsal pro-
minence posterolateral to the prothoracic shield with transverse row of
prominent setae. Fig. 8. Lateral view of prothoracic dorsum of *C.
(Mitoura) loki*. Note relatively high dorsal prominence posterolateral to
the prothoracic shield lacking transverse row of prominent setae. Scale
bar=0.1mm for figs. 3-6 and 1.0mm for figs. 7 and 8.

Figs. 9-14.   Sensory setae on prothoracic shield. Fig. 9. *Callophrys (M.) loki*. Fig.
10. *Plebulina emigdionis*. Fig. 11. *Apodemia mormo*. Fig. 12. *Callophrys (M.) spinetorum*. Fig. 13. *Euphilotes mojave*. Fig. 14. *Lycaena xanthoides*. Scale bar=0.1mm.
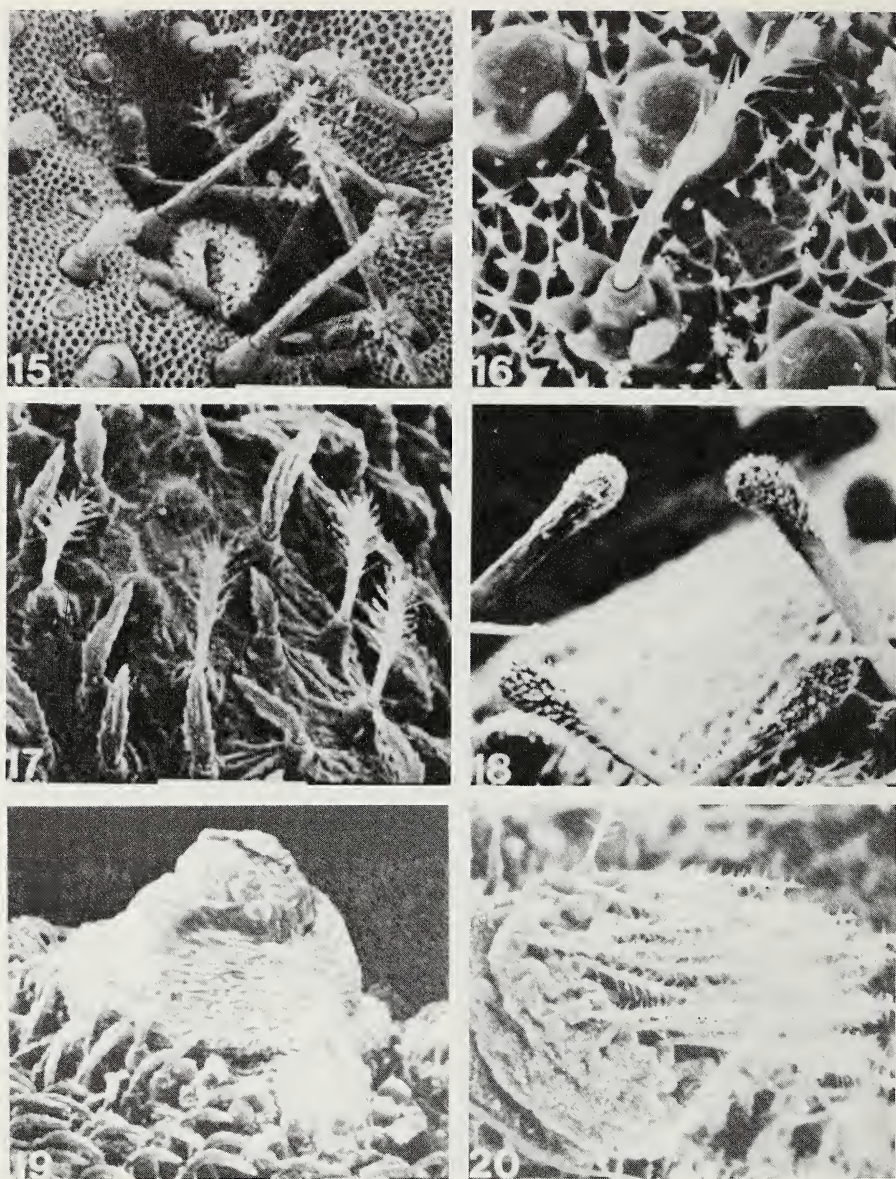
Figs. 15-20.   Dendritic setae, eversible tubercle, and honey gland. Fig. 15. Dendritic setae around A7 spiracle of *Lycaena xanthoides*; note lenticles, clavate-capitate setae, and mushroom setae. Fig. 16. Dendritic seta near A1 spiracle on *Celastrina argiolus*; note stellate chalaza and lenticles. Fig. 17. Dorsolateral dendritic setae on mesothorax of *Satyrium behrii*; note strongly dentate setae bent parallel to body surface. Fig. 18. Dendritic setae near honey gland of *Philotes sonorensis* (silk fiber across center). Fig. 19. Everted honey gland of *Euphilotes battoides*. Fig. 20. Partially everted eversible tubercle of *Celastrina argiolus*; note strongly spiculate setae at apex. Scale bar=0.01mm for figs. 16 and 18 and 0.1mm for all other figs.
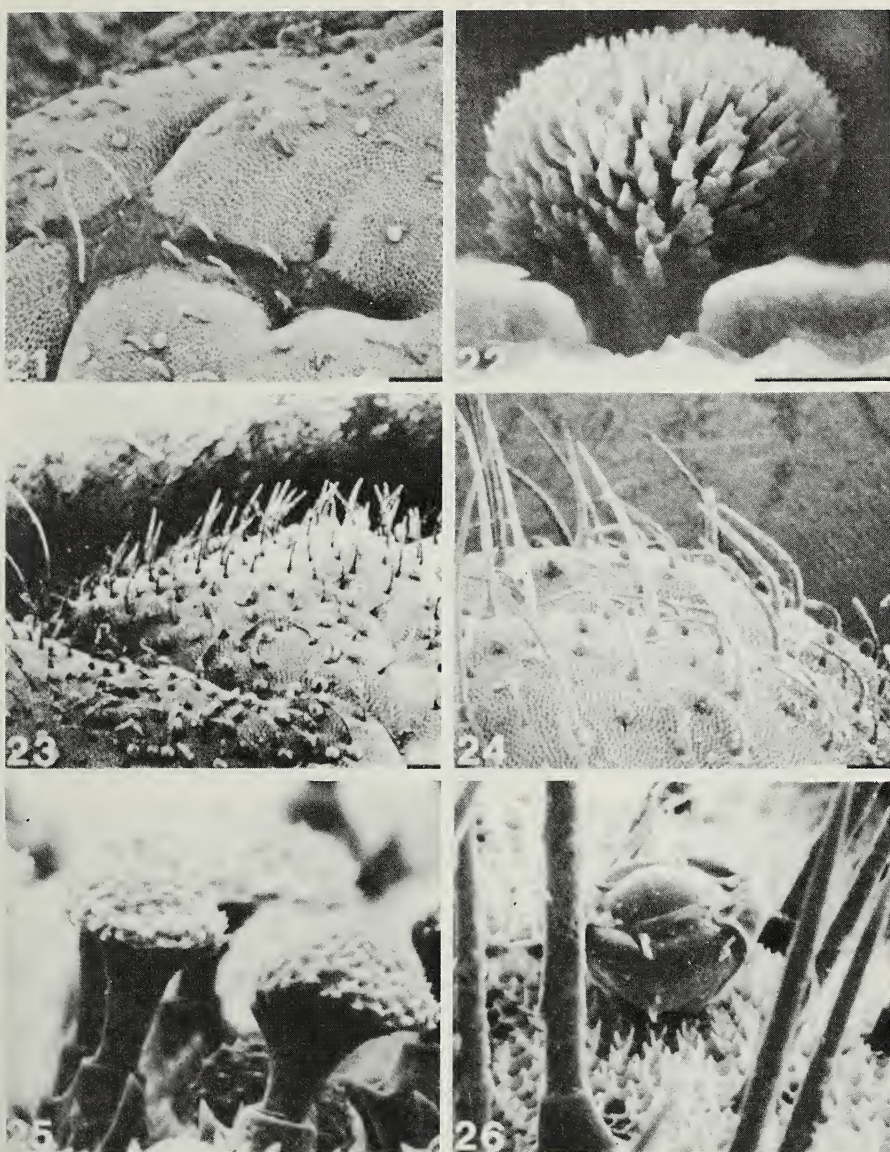
Figs. 21-26.   Fig. 20. *Lycaena hermes* prothoracic shield. Fig. 22. Mushroom seta of *Lycaena xanthoides*. Fig. 23. Lateral view of setae posterolateral to the prothoracic shield of *Lycaena arota*; note most setae directed caudad. Fig. 24. Lateral view of setae posterolateral to the prothoracic shield of *Lycaena nivalis*; note setae directed cephalad. Fig. 25. Capitate setae near honey gland of *Philotes sonorensis*. Fig. 26. Mushroom lenticle of *Atlides halesus*. Scale bar=0.1mm for figs. 21, 23, and 24 and 0.01mm for figs. 22, 25, and 26.
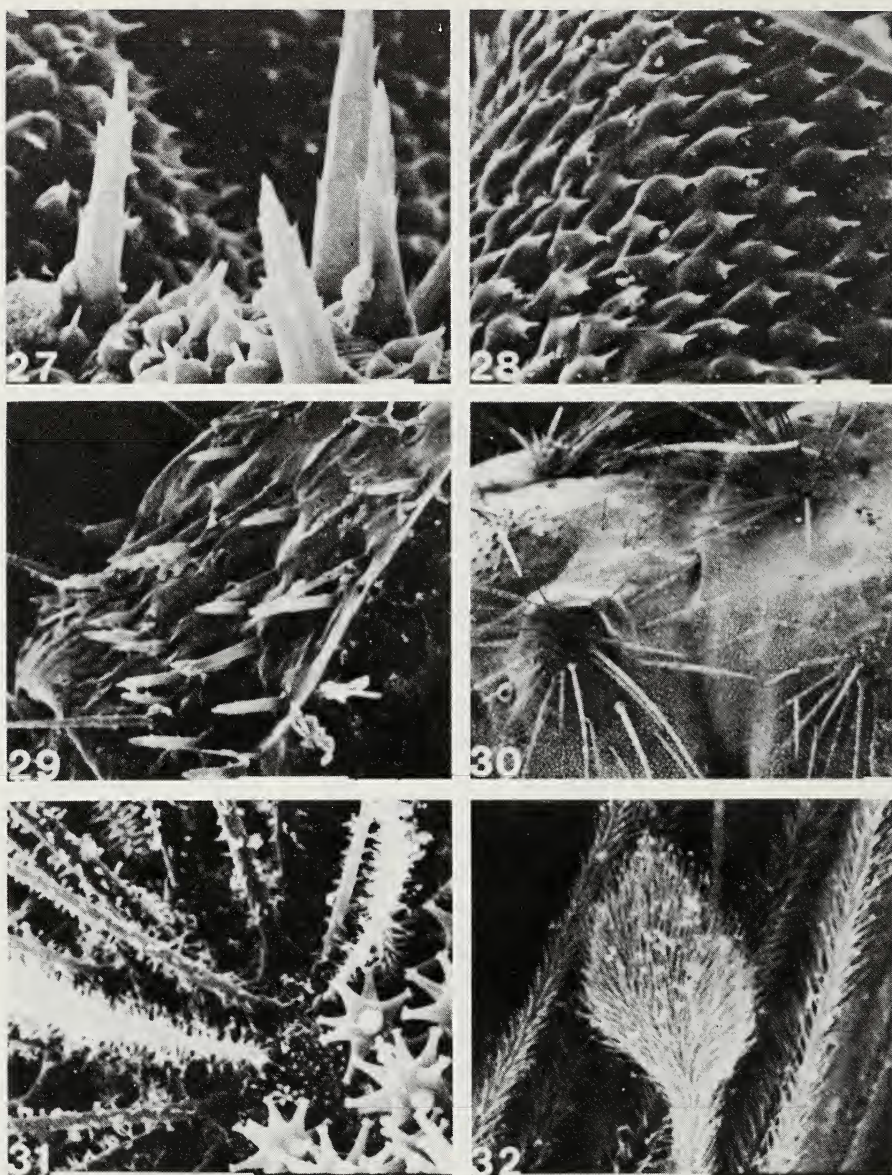
Figs. 27-32.   Various setae and spinules. Fig. 27. Neck setae and spinules of
Callophrys (M.) johnsoni. Fig. 28. Spinules on neck of *Plebulina
emigdionis*. Fig. 29. Setae on the frons of *Callophrys (I.) mossii*. Fig.
30. Lateral view of abdominal segments one and two of *Apodemia
mormo*; note A1 spiracle anteroventral to lateral verruca. Fig. 31.
Dorsal verruca of *Calephelis nemesis*; note echinoid (lower right)
and plumose setae. Fig. 32. Spatulate tip of plumose seta of
Calephelis nemesis. Scale bar=0.01mm for figs. 27, 28, and 32 and
0.1mm for figs. 29-31.
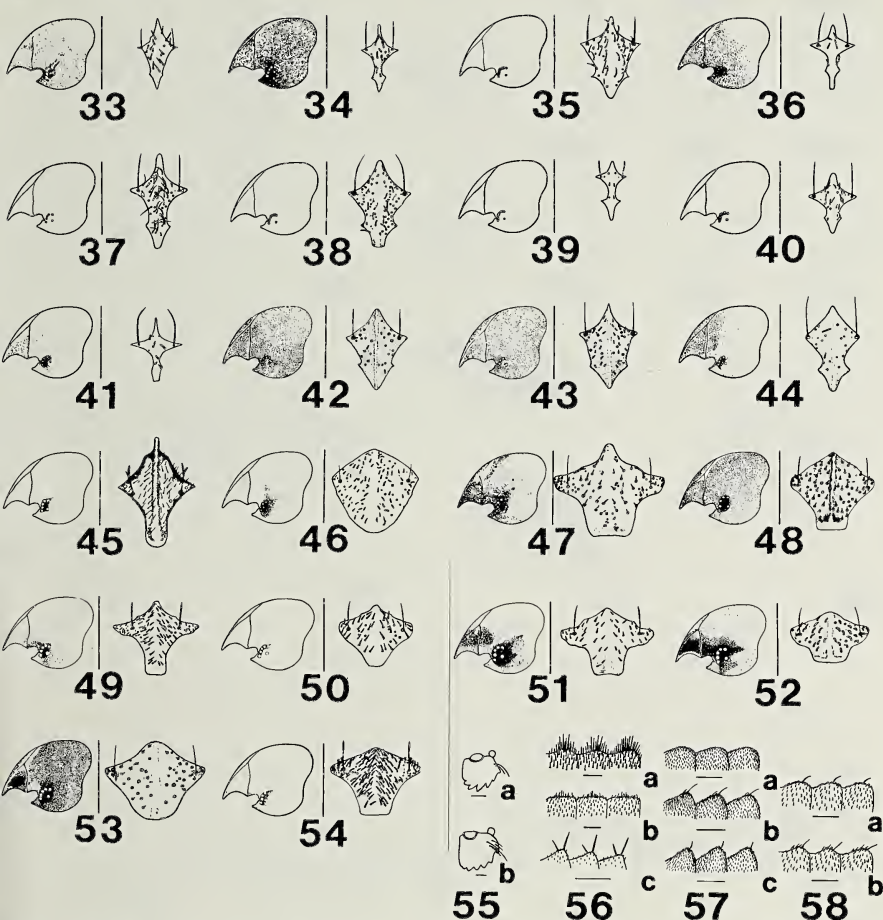
Figs. 33-44.   Cranial pigmentation (left) and prothoracic shields (right) for 12
                Lycaena species. Fig. 33. *L. phlaeas*. Fig. 34. *L. cupreus*. Fig. 35. *L.
                arota*. Fig. 36. *L. nivalis*. Fig. 37. *L. gorgon*. Fig. 38. *L. heteronea*. Fig.
                39. *L. hermes*. Fig. 40. *L. helloides*. Fig. 41. *L. mariposa*. Fig. 42. *L.
                editha*. Fig. 43. *L. rubidus*. Fig. 44. *L. xanthoides*. Scale bar=1mm
                for prothoracic shield; crania not drawn to scale.

Figs. 45-54.   Cranial pigmentation (left) and prothoracic shields (right) of *Atlides,
                Habrodais, Harkenclenus*, and *Satyrium* species. Fig. 45. *A. halesus*.
                Fig. 46. *H. grunus*. Fig. 47. *H. titus*. Fig. 48. *S. fuliginosum*. Fig. 49. *S.
                saepium*. Fig. 50. *S. sylvinus*. Fig. 51. *S. auretorum*. Fig. 52. *S. behrii*.
                Fig. 53. *S. californica*. Fig. 54. *S. tetra*. Scale bar=1mm for prothoracic
                shields; crania not drawn to scale.

Fig. 55.   Mandibular setation of *Satyrium saepium* and *Lycaena xanthoides*,
                aboral surface of left mandibles. Fig. 55a. *S. saepium*. Fig. 55b. *L.
                xanthoides*. Scale bar=0.1mm.

Fig. 56-58.   Dorsal profile and setae of abdominal segments 1-3 of *Satyrium tetra,
                S. auretorum, Ministrymon leda, Euphilotes enoptes, E. mojave, E.
                rita, Hemiargus ceraunus,* and *H. isola*. Fig. 56a. *S. tetra*. Fig. 56b. *S.
                auretorum*. Fig. 56c. *M. leda*. Fig. 57a. *E. enoptes*. Fig. 57b. *E.
                mojave*. Fig. 57c. *E. rita*. Fig. 58a. *H. ceraunus*. Fig. 58b. *H. isola*.
                Scale bar=1mm.
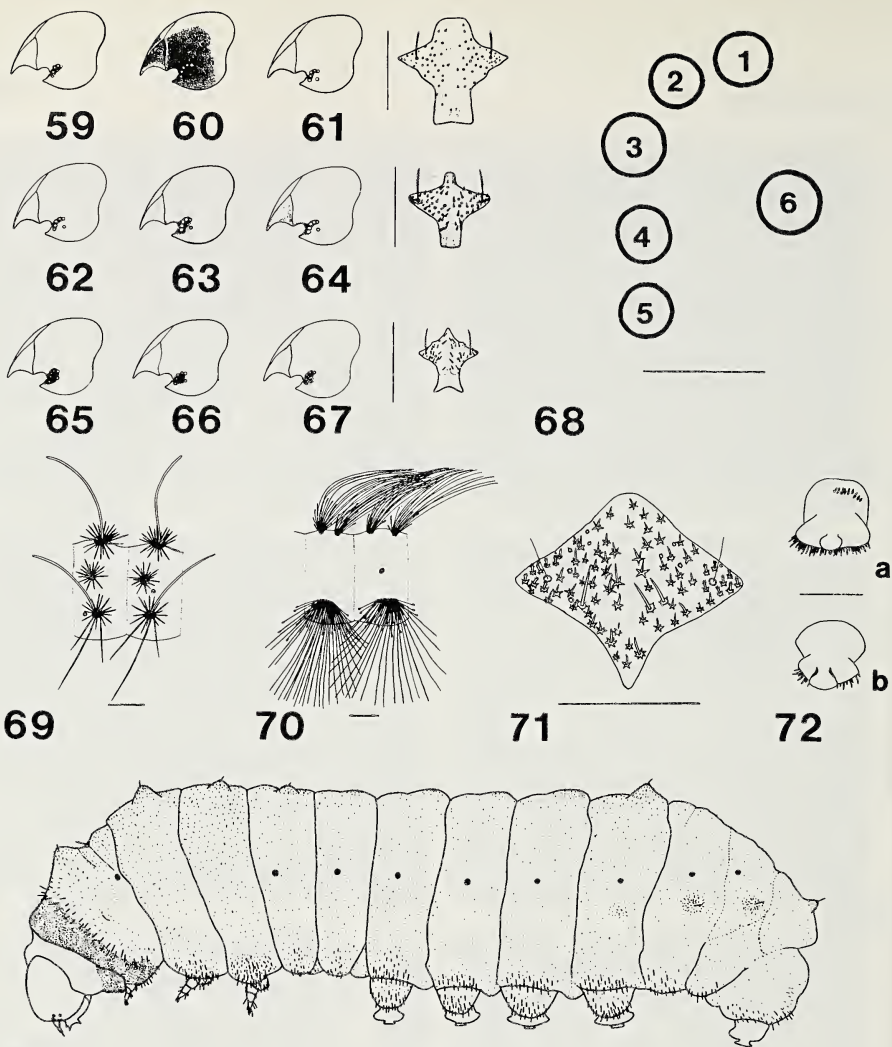
Figs. 59-67.   Cranial pigmentation and prothoracic shields of some *Callophrys* and *Strymon* species. Fig. 59. *C. perplexa* cranium. Fig. 60. *C. comstocki* cranium. Fig. 61. *C. (Mitoura) spinetorum* cranium (left) and prothoracic shield (right). Fig. 62. *C. (Incisalia) augustus* cranium. Fig. 63. *C. (I.) fotis* cranium. Fig. 64. *C. (I.) mossii* cranium (left) and prothoracic shield (right). Fig. 65. *S. avalona* cranium. Fig. 66. *S. columella* cranium. Fig. 67. *S. melinus* cranium (left) and prothoracic shield (right). Scale bar=1mm for prothoracic shields; crania not drawn to scale.

Fig. 68.   *Lycaena xanthoides* ocelli; ocelli are numbered counterclockwise from the top. Scale bar=1mm.

Figs. 69, 70.   Lateral view of abdominal segments 1 and 2 of *Apodemia mormo* and *Calephelis nemesis* showing placement of spiracles and verrucae. Fig. 69. *A. mormo*. Fig. 70. *C. nemesis*. Scale bar=1mm.

Fig. 71.   Prothoracic shield of *Icaricia lupini*. Scale bar=1mm.

Fig. 72.   Planta of prolegs of *Habrodais grunus* and *Everes amyntula*. Fig. 72a. *H. grunus*; note short series of lateral crochets. Fig. 72b. *E. amyntula*; note pigmented basal margins of spatulate lobe. Scale bar=0.5mm.

Fig. 73.   Distended last instar *Callophrys (Mitoura) spinetorum* larva. Note prominent setae confined to dorsal and lateral prominences, other setae very short and sparse. Scale bar=1mm.

Fig. 74. Larval photographs of 40 lycaenid species. Species are listed from left to right(a-d) by row (1-10) from the top. Row 1: a) *A. mormo*, b) *A. palmerii*, c) *C. nemesis*, d) *L. arota*; row 2: a) *L. gorgon*, b) *L. hermes*, c) *L. heteronea*, d) *L. mariposa*; row 3: a) *L. nivalis*, b) *L. phlaeas*, c) *L. xanthoides*, d)*H. grunus*; row 4: a) *A. halesus*, b) *C. (C.) dumetorum*, c) *C. (C.) perplexa*, d) *C. (I.) augustus*; row 5: a) *C. (I). eryphon*, b) *C. (M.) nelsoni*, c) *C. (M.) spinetorum*, d) *H. titus*; row 6: a) *M. leda*, b) *S. auretorum*, c) *S. behrii*, d) *S. californica*; row 7: a) *S. fuliginosum*, b) *S. sylvinus*, c) *S. tetra*, d) *A. franklinii*; row 8: a) *B. exilis*, b) *C. argiolus*, c) *E. battoides*, d) *E. rita*; row 9: a) *G. lygdamus*, b) *G. piasus*, c) *H. isola*, d) *I. shasta*; row 10: a) *L. melissa*, b) *P. sonorensis*, c) *P. speciosa*, d) *P. emigdionis*. All subjects greater than life size. Orientation is standard (cephalad at left) except 1d, 2d, 5a, 7b, 8c, and 9d with cephalad at right.